Gimme Shell-ter: Abundance, age/size structure and fecundity of *Pecten maximus* and *Aequipecten opercularis* inside and outside a temperate no take zone

ABSTRACT: The effectiveness of strict spatial protection as a shellfish fisheries management tool was examined through the collection and measurement of two sample sets of two commercially harvested pectinid species: Pecten maximus and Aequipecten opercularis. One sample set was collected from locations inside an unfished "no take zone" in the Firth of Clyde, Scotland and the other from fished locations surrounding this reserve; sampled P. maximus individuals inside the reserve were 1.4 times older and 1.3 times larger than those sampled outside, with A. opercularis displaying the same differences in age and size. Exploitable biomass was 1.6 times higher among sampled P. maximus inside the reserve and 2 times higher among A. opercularis individuals, with similar scale differences observed for both species' reproductive biomass. In spite of these clear differences in age, size and biomass, neither species was found to be more abundant inside the reserve nor was consistent evidence found that reserve populations were exhibiting faster growth characteristics than those outside. The lack of strong comparative density patterns is attributed to minimal scallop fishery pressure in the "fished" sample locations and possible population stability engendered by the older, larger protected individuals. A broader, "network" approach of reserves is recommended for the area's shellfish fisheries, in line with similar methodologies implemented in the Irish Sea.

1. Introduction

Commercially exploited mollusc species make up 7.2% of global capture fishery production, 12.7% of which comprises individuals of species in the Pectinidae family, or scallops (Food and Agriculture Organization of the United Nations [FAO], 2011). In the United Kingdom (UK), scallop capture production has risen by an average 5.6% (SD=15.0%) per year since 1980 and by 25.6% (SD=1.7%) per year since 2009, totalling 55,092 tonnes of landings in 2011 (FAO, 2011). UK scallop fisheries are worth over £63 million per year, making them the third most valuable in the country, behind only those for Atlantic mackerel (*Scomber scombrus*) and Norway lobster (*Nephrops norvegicus*) (Marine Management Organisation [MMO], 2012).

UK fisheries for king scallops (*Pecten maximus*) originated in the coastal waters of the Firth of Clyde in the 1930s, when 10 inshore dredging vessels operated seasonally in winter months (Dobby *et al.,* 2012). Similar fisheries spread across the Scottish west coast in the 1970s, also coinciding with the introduction of this target species in inshore English and Welsh fisheries (Franklin *et al.,* 1980). Queen scallops (*Aequipecten opercularis*) have been utilised as a source of bait in Scottish fisheries since the 19th century (particularly in the Firth of Forth), only becoming a commercial target species themselves in the 1970s (Bailey *et al.*, 2000).

In recent years, the UK fishing sector's increasing financial reliance on scallop yields has necessitated attempts to quantify the status of stocks of *P. maximus* and *A. opercularis* in British waters. Beukers-Stewart and Beukers-Stewart (2009) concluded that, though variable, landings of both species were increasing at a rate suggestive of sustainable management, and that effort control measures in the principal fishing zones of west Scotland, the Irish Sea, the English Channel and Moray Firth had successfully curbed observed declines in the 1990s. However, a subsequent report by the Scottish government – utilising time series analysis (TSA) stock assessments for the first time for this species in UK waters – revealed that poor recruitment since the mid 1990s has depleted unexploited biomass in west coast stocks and

that current levels of fishing intensity may therefore be unsustainable (Dobby *et al.,* 2012).

As with the decline of any targeted marine species, the possible depletion of the UK's scallop stocks necessitates the application and/or adaptation of fisheries management tools to attempt to stabilise commercially exploited populations. Whilst this has traditionally involved the use of population biomass indices such as maximum sustainable yield (MSY) in order to set vessel effort at appropriate levels, spatial protection measures in the form of marine protected areas (MPAs) have emerged as a significant addition to stock management, satisfying both economic and conservation aims (Roberts *et al.,* 2005). Though MPAs offer highly variable forms of protection, strict marine reserves prohibiting extractive activities such as fishing (also referred to as "no take zones" [NTZs]) have been shown globally to dramatically increase the density, age/size structure and fecundity of target and non-target species (Lester *et al.,* 2009), with these expanding populations also supplying neighbouring fishing grounds through the "spill-over effect" (McClanahan & Mangi, 2000; Ashworth & Ormond, 2005).

Given their limited mobility and relatively long pelagic larval phase, scallops are particularly appropriate candidates for spatial protection; protected populations have been observed to expand in size, age structure and fecundity within reserve boundaries and subsequently seed other populations in neighbouring zones, promoting fisheries recovery and/or stability in these areas (Nicolle *et al.,* 2013). One of the most notable examples is the Port Erin Closed Area in the Isle of Man, where *P. maximus* densities increased by 7 times over 14 years of protection, with exploitable and reproductive biomass increasing by 11 and 12.5 times respectively (Beukers-Stewart *et al.,* 2005). Similar levels of increased scallop biomass have been observed within seasonal closed areas in other locales such as the Canadian section of Georges Bank and Mexico's San Jorge Island in the Gulf of California (Murawski *et al.*, 2000; Cudney-Bueno *et al,*, 2009).

With a growing body of evidence to support the effectiveness of MPAs – as well as the target issued by the Convention on Biological Diversity (CBD) for 17% of the world's oceans to be safeguarded through a network of protected areas – many nations are formalising (or have enacted) plans to confer some level of protection on sections of seas within their jurisdiction. For its part, the Scottish government is currently consulting on proposals for a network of 33 MPAs whose designation is intended to answer a variety of objectives, including management of large, charismatic species such as the basking shark (*Cetorhinus maximus*), which are resident in Scottish waters (Scottish Natural Heritage [SNH], 2013). It is worth noting that in its online publicity surrounding the consultation, the Scottish government states that "MPA measures are not a fisheries management tool. Mechanisms already exist for that purpose. However fisheries restrictions may be required at some MPAs" (The Scottish Government, 2013).

However, the potential long-term fisheries and biodiversity benefits of strict spatial protection can be tested in Scottish waters through study of the Lamlash Bay NTZ on the Isle of Arran, in North Ayrshire, west Scotland. This community-conceived and managed NTZ was designated in 2008, largely through the efforts of the Community of Arran Seabed Trust (COAST), a local non-governmental organisation (NGO); the protected area prohibits "all fishing for sea fish" (Scottish Government Marine Directorate, 2008). Given the exclusion of marine reserves/no take zones from both the Scottish MPA proposals and the English and Welsh Marine Conservation Zone (MCZ) project, the Lamlash Bay NTZ can provide a vital insight into the effectiveness of strict protection in restoring biodiversity and improving fishery yields in a temperate environment. The present study will focus on the fisheries benefits of the NTZ by contrasting the density, size, age structure and fecundity of individuals of both exploited species of scallop (*P. maximus* and *A. opercularis*) inside and outside the NTZ, making further considerations of the growth characteristics of the two sampled populations and the impact of environmental variables on scallop density. The study will conform to a basic "control VS impact" experimental design, wherein the study locations within

the designated NTZ represent the "impact" of fishing cessation and those outside represent the "control", where fishing activity continues.

2. Method

2.1 Study site

Lamlash Bay NTZ covers a 2.67km^2 area of coastal sea between the village of Lamlash on the east side of the Isle of Arran, Scotland, UK and the west side of neighbouring Holy Isle (Howarth *et al.*, 2011). The NTZ boundary is demarcated by the points of Mount Pleasant Farm, Clauchlands Point and Hamilton Rock on Arran and Holy Isle West and Holy Isle East on Holy Isle (Fig. 1). Water depth ranges from 11.3 to 43m below chart datum, the majority being less than 20m (Axelsson *et al.,* 2010).

Figure 1. Boundary of the Lamlash Bay NTZ (from Axelsson *et al.,* 2010).

Axelsson et al (2010) identified 10 substrate biotopes across the three spatial zones of "Northern Lamlash Bay and North Channel", "Central and southern Lamlash Bay" and "Outer Lamlash Bay". The first of these zones was dominated by "mixed sediments" substrate (defined as "muddy, gravelly sands with shell material") and the second and third zones were dominated by "muddy sand". "Mixed sediments" was the most frequently occurring substrate type across all three zones.

Given the variability of depth and habitat type across the NTZ, a representative range of study locations within the site was chosen, with a further range of control locations of equivalent depth and habitat type outside the NTZ – as far as was practicably possible – selected to match each study location. 16 study locations were identified inside the NTZ and 16 control locations outside, making a total of 32 locations (Fig. 2).
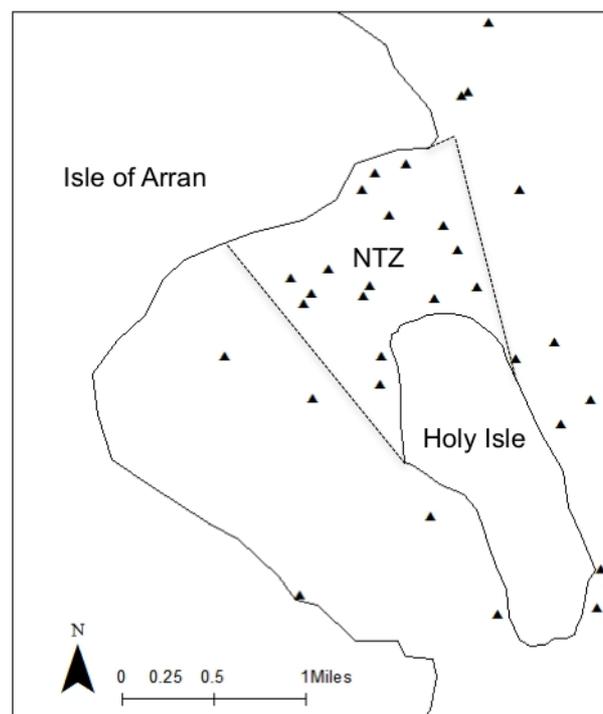

Figure 2. Spatial distribution of the 32 study locations inside and outside the NTZ.

2.2 Dive surveys

Field work took place between 5th July and 20th August 2013, aboard the COAST vessel *Cowal* and encompassed a total of 32 dives, one per location. In order to assess scallop abundance, size and age, the 16 study locations and 16 control locations were surveyed by two SCUBA divers, using a 3m by 50m (150m^2) band transect methodology to collect individuals in situ for subsequent counting, aging and measurement. After utilising GPS start and end transect co-ordinates previously recorded by Howarth et al (2011) to arrive at a location, a 50m rope transect line – anchored at either end and marked on the surface by buoys – was laid by dropping one anchored end at the location and then reeling out the line whilst the vessel reversed in a straight line, maintaining the same depth profile across the transect. Once unreeled, the other anchored end was dropped and the transect was set.

The width of the band transect was demarcated through the use of a 3m plastic pipe, the centre of which was marked with white tape. The pipe was held at each end by a diver and moved along the transect line, keeping the tape aligned with the position of the marker rope. When a *P. maximus* or *A. opercularis* individual was sighted within the band transect, the pipe was carefully placed onto the substrate and the scallop picked up and placed into a lightweight mesh bag. Additionally, both divers recorded bottom water temperature and depth using Suunto Zoop dive computers, noted the typology of the substrate and completed abundance counts of common species as well as SACFOR scale abundance estimates for colonial organisms (Joint Nature Conservation Committee [JNCC], 1990). For the abundance counts, tallies were made against prepared species lists of crustaceans (*Liocarcinus depurator*, *Pagurus* spp., *Cancer pagurus*, *Munida rugosa*, *Necora puber* etc.), echinoderms (*Asterias rubens*, *Crossaster papposus*, *Ophiuroidae* spp., *Crinoidea* spp. etc.), teleosts (*Gadus morhua*, *Melanogrammus aegelfinus*, *Merlangius merlangus* etc.), molluscs (*Ensis arcuatus*, *Turritella communis* etc.) and marine worms (*Chaetopterus variopedatus*, *Myxicola infundibulum* etc.). For the SACFOR scales, the relative abundance was estimated for dead and live maerl (*Lithothamnion corallioides*, *Lithothamnion glaciale* and *Phymatolithon calcareum*), macroalgae (*Laminaria* spp., *Fucus* spp. etc.),

sponges (*Halichondoria panicea*, *Pachymatisma johnstonia*, *Suberites ficus* etc.), tunicates (*Clavelina lepadiformis*, *Ciona intestinalis* etc.), hydroids (*Nemertesia* spp., *Tubularia indivisa* etc.), bryozoans (*Bugula plumosa*, *Conopeum reticulum* etc.), anemones (*Cerianthus lloydi*, *Metridium senile* etc.) and corals (*Alcyonium digitatum*, *Caryophyllia smithii* etc.).

Back on the vessel, collected *P. maxmimus* and *A. opercularis* individuals were identified, counted, measured and aged. The widest point of each individual's shell was recorded in millimetres and the relevant side of those shells was then scrubbed with a wire brush in order to reveal growth rings; these were counted to give each individual's age in years. Individuals were returned to the study location after measurement.

2.3 Laboratory analysis

In order to assess scallop fecundity, 60 *P. maximus* and 60 *A. opercularis* individuals were retained for dissection, with half of the collected individuals of each species collected in the NTZ, half from outside. Individuals were preserved in seawater and dissected within 24 hours. After separation, the wet weight of those tissues representing muscle biomass (the adductor), reproductive biomass (the gonads) and exploitable biomass (adductor and gonad weight summed) were recorded using an electronic balance.

2.4 Data analysis

2.4.1 Density

Total counts of *P. maximus* and *A. opercularis* individuals at each study location were converted to measures of density in number of individuals per 100m^2. This was achieved through dividing the total counts by the number of square metres surveyed (150 for all locations) and then multiplying that figure by 100. The resulting density measures did not conform to a normal, Gaussian distribution and therefore the non-parametric Mann-Whitney-Wilcoxon summed ranks test was used to assess any statistical differences between mean densities inside and outside the NTZ.

Separate density measures were also calculated for individuals below and equal to or above legal landing limits (*P. maximus* ≥ 100mm: Keltz & Bailey, 2012; none in place for *A. opercularis*, but Isle of Man government utilises ≥ 50mm: Department of Environment, Food and Agriculture, 2010). These separate density measures were also assessed using Mann-Whitney-Wilcoxon tests. All statistical tests described in sections 2.4.1 – 2.4.4 utilised the statistical software R (version 3.0.1; http://www.R-project.org/).

2.4.2 Age, shell size and composition

Distribution plots of size and age groups were created for populations of both species within and outside the NTZ. The resulting size and age distributions were compared using Kolmogorov-Smirnov distribution tests. Differences in mean shell size and age of both species inside and outside the NTZ were tested using Student's T-test.

2.4.3 Exploitable and reproductive biomass

The relationships between shell size and exploitable biomass were plotted utilising the measurements taken from the 30 sampled individuals of each species and from each population (inside and outside the NTZ). The process was repeated for the relationships between shell size and reproductive biomass in each population and species. Power trendlines were fitted to these relationships and – assuming that a sufficient proportion of variance in the data was accounted for ($R^2 ≥ 0.7$) – the equations of these power lines were applied to all sampled individuals. Utilising the sampled shell sizes, theoretical exploitable and reproductive biomass values were derived for each individual of each species and each population.

Mean exploitable biomass and reproductive biomass were then compared for each species utilising a Mann-Whitney-Wilcoxon test.

2.4.4 Environmental variables

Total counts of key observed non-pectinid species (especially those known to exert scallop predation pressure such as *C. pagurus* and *A. rubens*) at each study location were converted to measures of density in number of individuals per 100m^2. Overall study location biodiversity was calculated through converting species abundance lists into Shannon's diversity and equanimity measures. Substrate typologies were transformed into a structural complexity scale in which locations where boulders were present were taken to be most complex and locations dominated by sandy mud least complex (Table 1).

Table 1. Observed substrate characteristics and converted structural complexity rating.

Key substrate characteristic	Structural complexity rating
Sandy mud	1 (least complex)
Presence of shells	2
Presence pebbles	3
Presence of cobbles	4
Presence of maerl (including dead)	5
Presence of boulders	6 (most complex)

Each of these variables – as well as level of protection (i.e. inside the NTZ or outside), depth, temperature and the SACFOR abundance scales – was modelled against *P. maximus* and *A. opercularis* density to observe which, if any, best predicted scallop abundance. Variables were first plotted in isolation and appropriate transformations were applied to remove skew and attempt to conform the data to a normal distribution. Pearson's correlation co-efficient (*r*) and variance inflation factor (VIF) tests were used to identify intercorrelation between predictor variables, with $| r | \geq 0.7$ and/or VIF ≥ 5.0 taken to signify intercorrelation (Zuur *et al.*, 2010).

These test results were then used to create three sub-sets of uncorrelated variables which then formed three multivariate generalised linear models (GLMs), used to determine the significance of each predictor variable in each set. As overdispersion was present in these initial models, negative binomial GLMs were instead used, as these are robust to overdispersion. These

multivariate GLMs were then reduced using backwards-forwards stepwise selection, using Akaike Information Criteria (AIC) to determine which variable combinations, in which order, best explained the response variables. A Chi-square goodness of fit test was then performed on each reduced model to determine whether it explained significantly less of the deviance in the response variable and the Bonferroni correction was applied to account for repetitive testing (Dunn, 1961).

2.4.5 Growth rates

Mean length at age was plotted for the sampled populations of *P. maximus* and *A. opercularis* and the statistical software Simply Growth (version 1.7, http://www.pisces-conservation.com/) was used to fit Von Bertalanffy growth curves to the separate populations of each species. The log-likelihood ratio test of co-incident curves (Kimura, 1980) was used to test whether the two sampled population curves for each species differed from a curve created by combining the two sampled populations. In order to observe whether any divergence in growth rates between populations was taking place in young scallops (i.e. at size-at-age levels below legal landing size limits, when the compounding effect of fishing mortality should be minimised), one way ANOVAs were used to compare mean size at age in 2 and 3 year old *P. maximus* and 1 and 2 year old *A. opercularis*.

3. Results

3.1 Total individuals collected

147 *P. maximus* and 74 *A. opercularis* individuals were collected from inside the NTZ across 16 study locations, compared to 124 and 73 individuals outside the NTZ across 16 control locations, respectively.

3.2 Density

P. maximus mean density was 6.13 individuals per $100m^2$ in the NTZ (±SE = 1.57, n=16) compared to 5.17 outside (±SE=1.73, n=16). This difference was not statistically significant (W=118.5, p=0.73, n=32). *A. opercularis* mean density was 3.08 per $100m^2$ in the NTZ (±SE=1.51, n=16), compared to 3.04 (±SE=0.75, n=16) outside. This difference was also not statistically significant (W=156.5, p=0.27, n=32). Fig. 3 shows these mean density values.
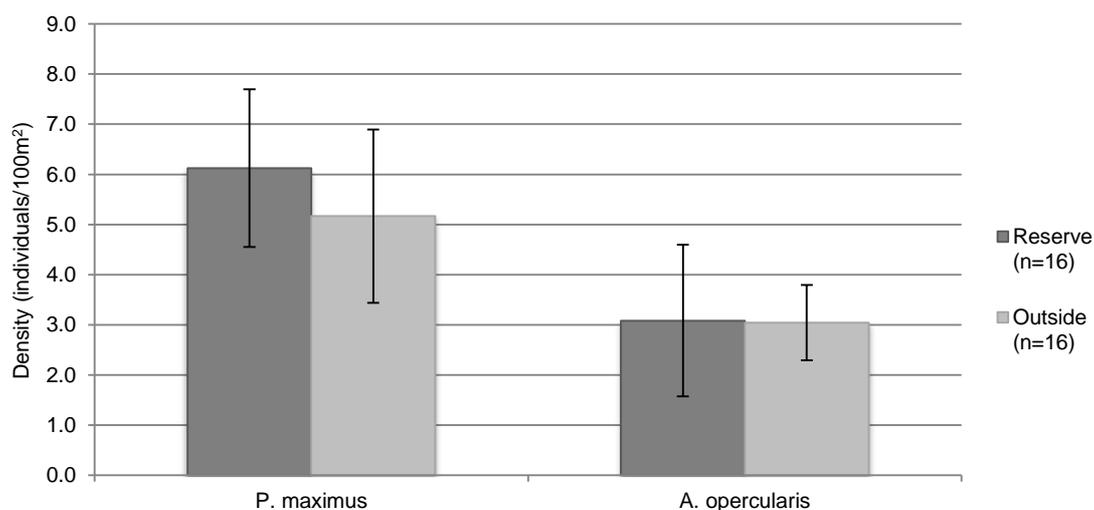

Figure 3. Mean scallop density within (n=16) and outside (n=16) the reserve for *P. maximus* and *A. opercularis*.

Legal size *P. maximus* mean density was 5.17 individuals per $100m^2$ in the NTZ (±SE = 1.40, n=16), compared to 2.75 outside (±SE=0.60, n=16). This difference was not statistically significant (W=108.5, p=0.47, n=32). Legal size *A. opercularis* mean density was 1.71 per $100m^2$ in the NTZ (±SE=0.86, n=16), compared to 0.83 (±SE=0.40, n=16) outside. This difference was also not statistically significant (W=109.5, p=0.43, n=32).

Sub-legal size *P. maximus* mean density was 0.38 individuals per 100m^2 in the NTZ (±SE = 1.71, n=16), compared to 2.17 outside (±SE=0.73, n=16). This difference was not statistically significant (W=156, p=0.24, n=32). No sub-legal size *A. opercularis* individuals were collected in the NTZ, compared to 0.60 (±SE=0.40, n=16) outside. Fig. 4 shows these legal and sub-legal mean density values.
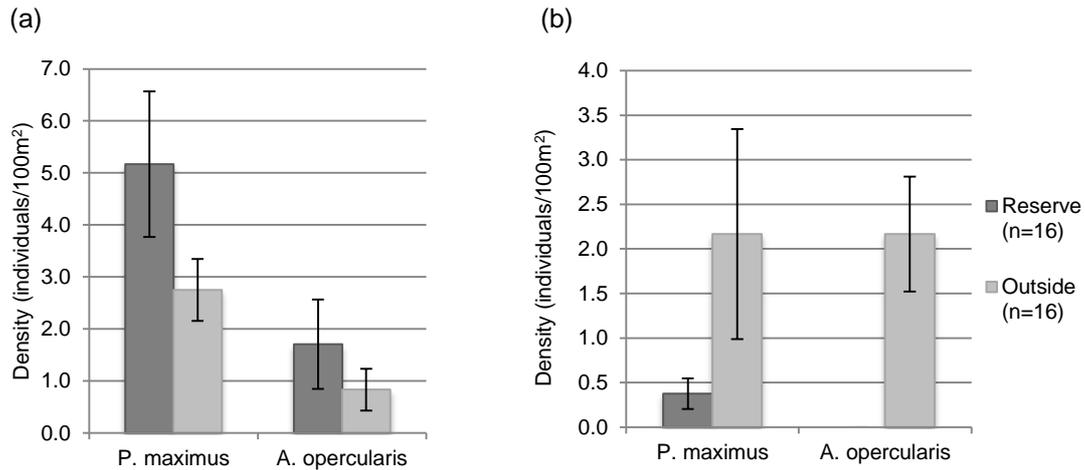

Figure 4. Mean densities within (n=16) and outside (n=16) the reserve for *P. maximus* and *A. opercularis* individuals of a) legal landing size and b) sub-legal landing size.

3.3 Shell size, age and composition

P. maximus size composition was dominated by larger individuals inside the NTZ and mid-size individuals outside the NTZ (Fig. 5). The distributions of sizes of *P. maximus* inside and outside the NTZ were found to be significantly different (D=0.46, p=<0.001). *A. opercularis* size composition was similarly dominated by larger individuals inside the NTZ and by smaller individuals outside (Fig. 6). The distributions of sizes of *A. opercularis* inside and outside the NTZ were found to be significantly different (D=0.31, p=0.002).
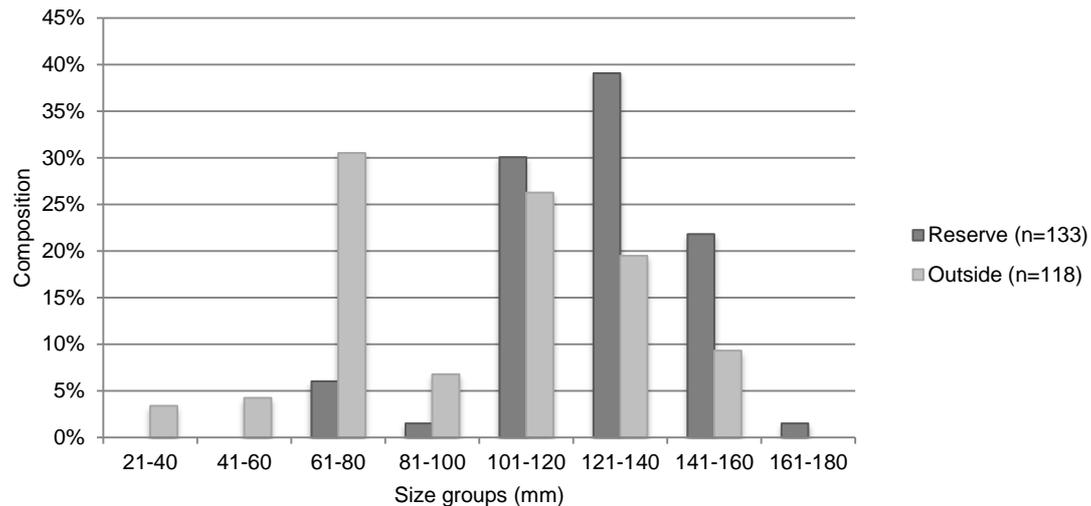
Figure 5. Composition of *P. maximus* by size group.

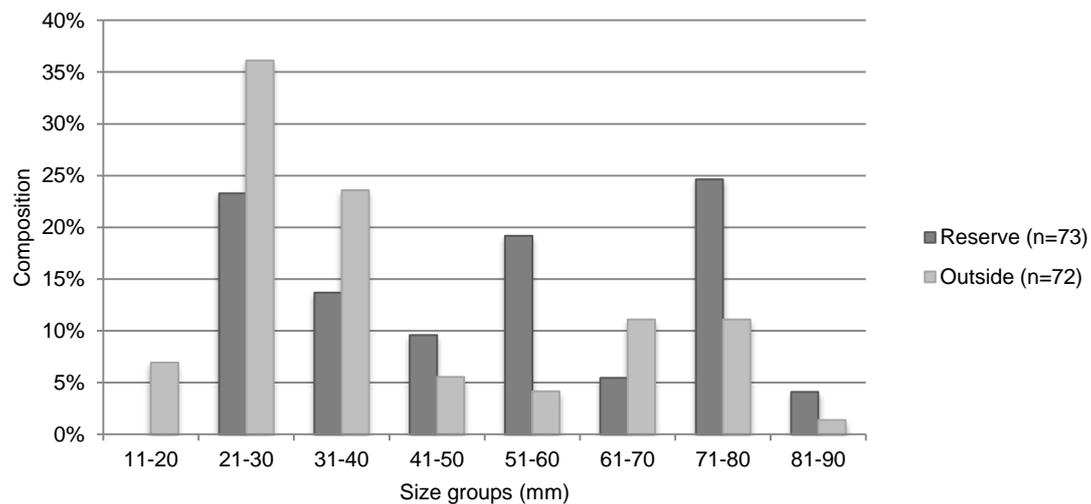Figure 6. Composition of *A. opercularis* by size group.

Overall, mean *P. maximus* shell size within the NTZ was 126.14mm (±SE=1.81, n=133) compared to 98.90 outside (±SE=2.90, n=118). Mean *A. opercularis* shell size within the NTZ was 51.07mm (±SE=2.35, n=73) compared to 40.39 outside (±SE=2.90, n=72). These differences between mean values were shown to be statistically significant (*P. maximus:* t=-7.96, d.f.=199, p=<0.0001; *A. opercularis:* t=-3.25, d.f.=142, p=0.0014), with shell size among both species 1.3 times higher in the NTZ. Fig. 7 shows these mean shell size values.
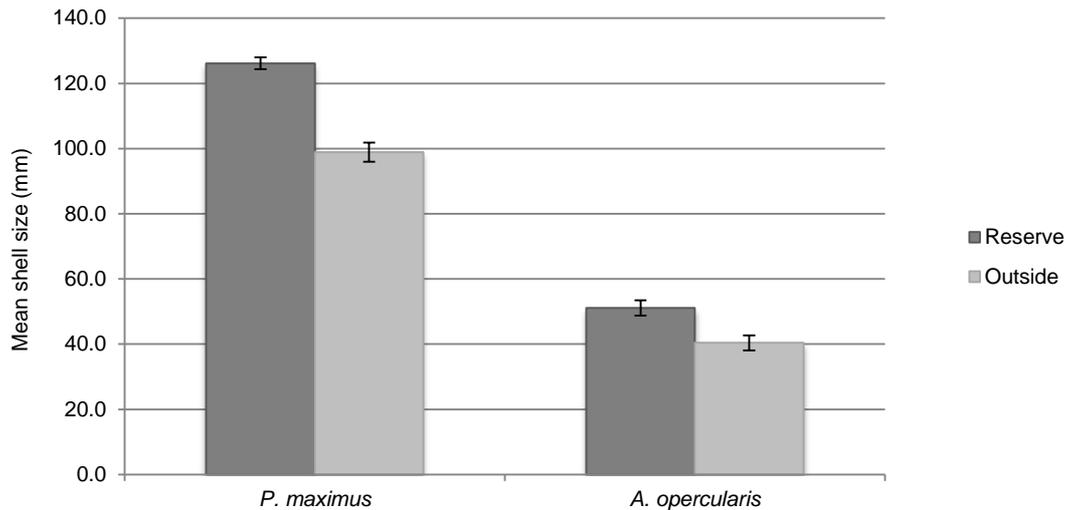
Figure 7. Mean scallop shell size of *P. maximus* within (n=133) and outside (n=118) the reserve and *A. opercularis* within (n=73) and outside (n=72) the reserve.

P. maximus age composition was dominated by older individuals inside the NTZ and younger individuals outside the NTZ (Fig. 8). The distributions of ages of *P. maximus* inside and outside the NTZ were found to be significantly different (D=0.39, p=<0.001). *A. opercularis* age composition was similarly dominated by older individuals inside the NTZ and by younger individuals outside the NTZ (Fig. 9). The distributions of sizes of *A. opercularis* inside and outside the NTZ were found to be significantly different (D=0.27, p=0.011).
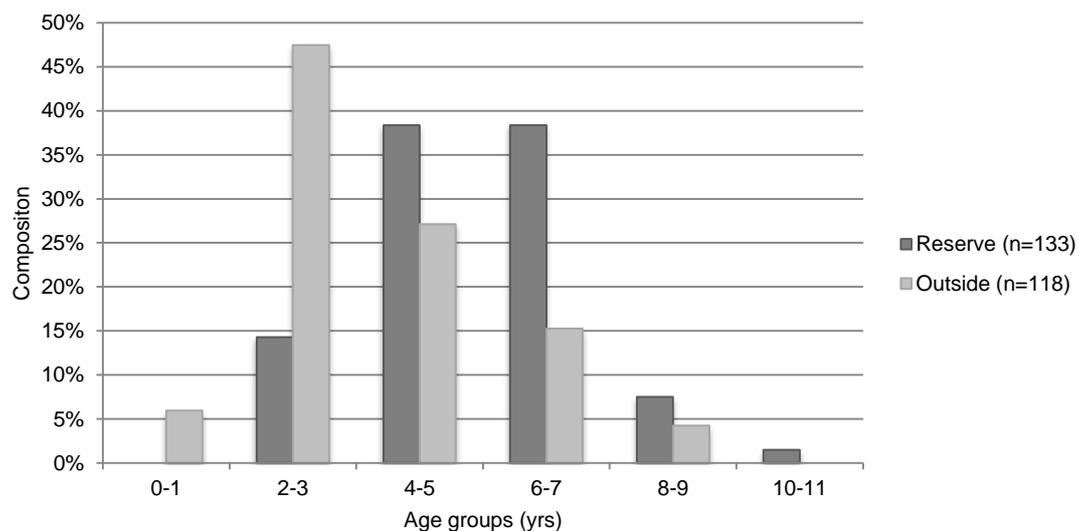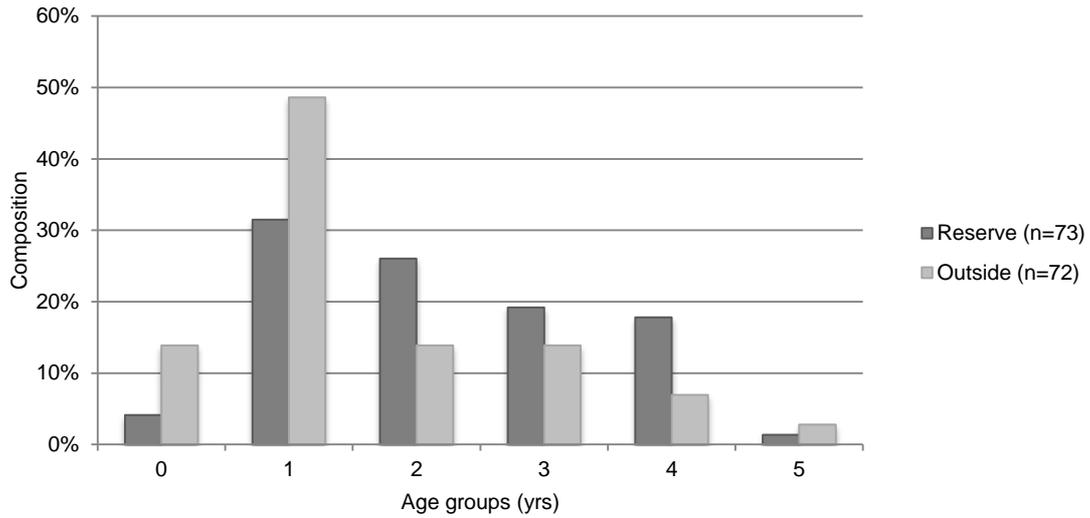

Figure 8. Composition of *P. maximus* by age group.

Figure 9. Composition of *A. opercularis* by age group.

Overall, mean *P. maximus* age within the NTZ was 5.23 years old (±SE=0.15, n=133) compared to 3.62 outside (±SE=0.18, n=118). Mean *A. opercularis* age within the NTZ was 2.19 (±SE=0.14, n=73) compared to 1.60 outside (±SE=0.15, n=72). These differences between mean values were shown to be statistically significant (*P. maximus:* t=-6.88, d.f.=239, p=<0.0001; *A. opercularis:* t=-2.89, d.f.=142, p=0.0044), with age among both species 1.4 times higher in the NTZ. Fig. 10 shows these mean age values.
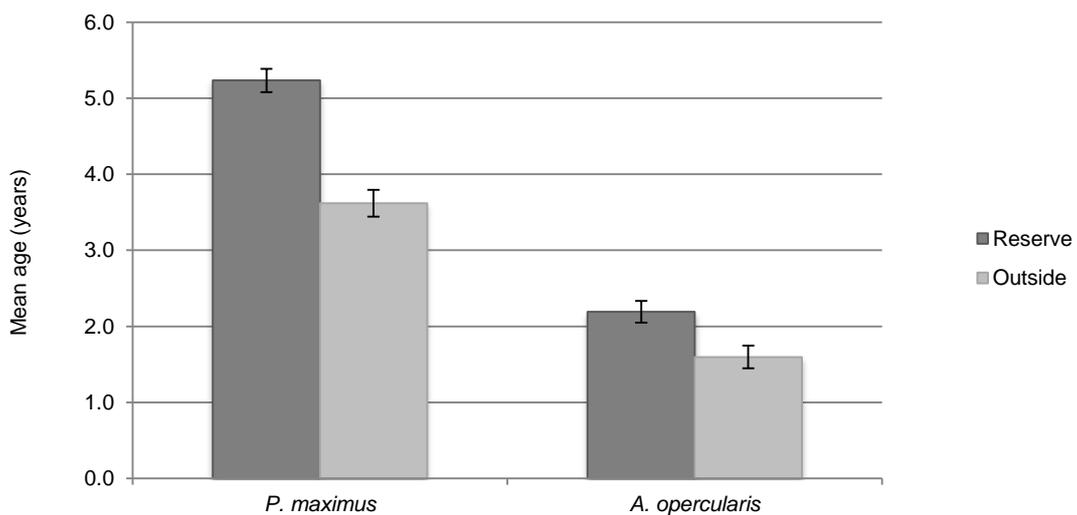

Figure 10. Mean scallop age of *P. maximus* within (n=133) and outside (n=118) the reserve and *A. opercularis* within (n=73) and outside (n=72) the reserve.

3.4 Exploitable and reproductive biomass

Each of the plotted relationships between reproductive and exploitable biomass of dissected individuals of both species from both populations (inside and out) was sufficiently statistically robust to extrapolate across non-dissected individuals. Trendline equations and measures of the strength of the relationships are presented in Table 2.

Table 2. Trendline equations and R^2 values for the biometric relationships between shell size and exploitable/reproductive biomass in reserve and outside populations of a) *P. maximus* and b) *A. opercularis*

	(a) Equation	R^2	(b) Equation	R^2
Reserve				
Exploitable biomass	$y = 3E\text{-}05x^{2.8952}$	0.92	$y = 2E\text{-}05x^{3.0570}$	0.88
Reproductive biomass	$y = 1E\text{-}07x^{3.7294}$	0.84	$y = 2E\text{-}06x^{3.3468}$	0.88
Outside				
Exploitable biomass	$y = 7E\text{-}06x^{3.1755}$	0.98	$y = 1E\text{-}05x^{3.1317}$	0.95
Reproductive biomass	$y = 2E\text{-}11x^{5.5836}$	0.94	$y = 8E\text{-}06x^{2.9758}$	0.93

Utilising these relationships to determine biomass for the entire sampled population, *P. maximus* mean exploitable biomass was 42.07g in the NTZ (±SE = 2.04, n=133), compared to 25.92 outside (±SE=2.39, n=118). This difference was statistically significant (W=3868, p=<0.001, n=251), with biomass 1.6 times higher in the NTZ. *A. opercularis* mean exploitable biomass was 5.89g in the NTZ (±SE=0.66, n=73), compared to 2.98 (±SE=0.46, n=72) outside. This difference was also statistically significant (W=1654, p=<0.001, n=145), with biomass 2 times higher in the NTZ. These mean biomass weights are compared in Fig. 11.

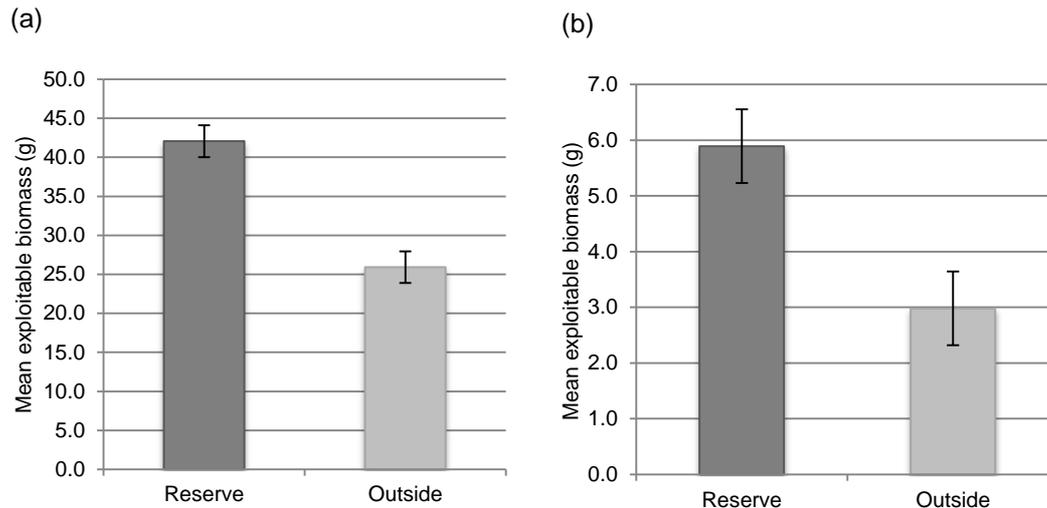(a)   (b)

Figure 11. Mean exploitable scallop biomass for a) *P. maximus* within (n=133, of which 31 directly measured and 102 extrapolated using biometrics) and outside (n=118, 30 measured and 88 extrapolated) the reserve and b) *A. opercularis* within (n=73, 37 measured and 36 extrapolated) and outside (n=72, 30 measured and 42 extrapolated) the reserve.

P. maximus mean reproductive biomass was 8.36g in the NTZ (±SE = 0.40, n=133), compared to 6.64 outside (±SE=0.81, n=118). This difference was statistically significant (W=4953, p=<0.001, n=251), with biomass 1.3 times higher in the NTZ. *A. opercularis* mean reproductive biomass was 1.60g in the NTZ (±SE=0.66, n=73), compared to 0.86 (±SE=0.46, n=72) outside. This difference was also statistically significant (W=1975, p=0.001, n=145), with biomass 1.9 times higher in the NTZ. These mean biomass weights are compared in Fig. 12.
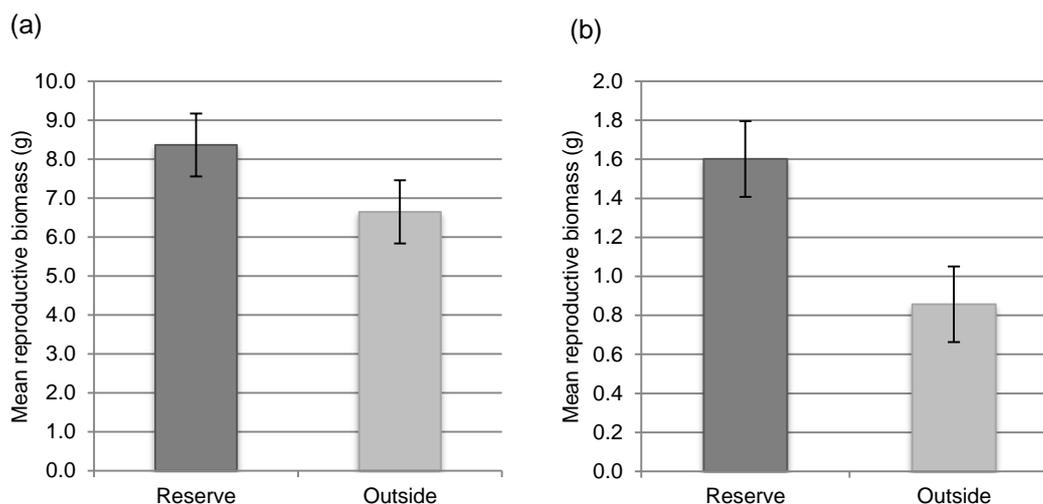
(a)

(b)

Figure 12. Mean reproductive scallop biomass for a) *P. maximus* within (n=133, of which 31 directly measured and 102 extrapolated using biometrics) and outside (n=118, 30 measured and 88 extrapolated) the reserve and b) *A. opercularis* within (n=73, 37 measured and 36 extrapolated) and outside (n=72, 30 measured and 42 extrapolated) the reserve.

3.5 Environmental variables

Each of the three reduced negative binomial GLMs found combinations of significant predictor variables that could adequately model *P. maximus* density (Table 3). The strongest of these variable combinations was *L. ciliaris* density and bryozoan SACFOR, though this last variable was intercorrelated with hydroid SACFOR, whose model revealed a more highly significant relationship. Seabed complexity was also revealed to be significant, however this third model did not account for much of the response variable's deviance.

Table 3. Predictors of *P. maximus* density at 32 sites at 95% level.

Significant variables	Test statistics	p-value (95% α=0.006)
Luidia ciliaris density +	AIC=165.93, %D=50.7	<0.0001
Bryozoans +	"	0.0001
Hydroids +	AIC=170.21, %D=49.8	<0.0001
Live maerl +	"	0.0006
Seabed complexity +	AIC=178.68, %D=31.1	0.0006

Each of the reduced models did not significantly alter the amount of deviance in the response variable explained (Table 4), meaning their use was justified.

Table 4. Results of goodness of fit tests for stepwise-reduced negative binomial GLMs for *P. maximus* density

Reduced model	χ^2	d.f.	p-value
Model 1	0.07	3	0.99
Model 2	2.80	5	0.73
Model 3	1.78	4	0.78

Two of the three reduced negative binomial GLMs found combinations of significant predictor variables that could adequately model *A. opercularis* density (Table 5). The model that best explained the deviance in the response variable combined *C. papposus* density and *Henricia* spp. density. Depth – though in a model that did not explain much deviance – was revealed to have the most highly significant relationship with *A. opercularis* density.

Table 5. Predictors of *A. opercularis* density at 32 sites at 95% level.

Significant variables	Test statistics	p-value (95% α=0.007)
Crossaster papposus density +	AIC=133.76, %D=46.9	0.003
Henricia spp. density +	"	0.004
Depth +	AIC=135.4 %D=35.6	<0.0001

The two reduced models that yielded relationships did not significantly alter the amount of deviance in the response variable explained (Table 6), meaning their use was justified.

Table 6. Results of goodness of fit tests for stepwise-reduced negative binomial GLMs for *A. opercularis* density

Reduced model	χ^2	d.f.	p-value
Model 1	2.84	3	0.42
Model 3	3.57	5	0.61

3.6 Growth rates

The Von Bertalanffy growth curves fitted to the mean size at age values for *P. maximus* revealed a higher growth rate (or, more accurately, rate of approach

to theoretical maximum size) among the NTZ population (k=0.32, L_∞=159.78, T_0=-0.09) compared to the population outside (k=0.28, L_∞=165.23, T_0=-0.14). The Kimura likelihood ration test of co-incident curves revealed that the two growth models were not significantly different from one another (RSS_ω=26966.97, X_2=7.66, d.f.=3, p=0.05) and, therefore, that the growth rates yielded by the curves were not comparable. The growth curves are shown in Fig. 13.
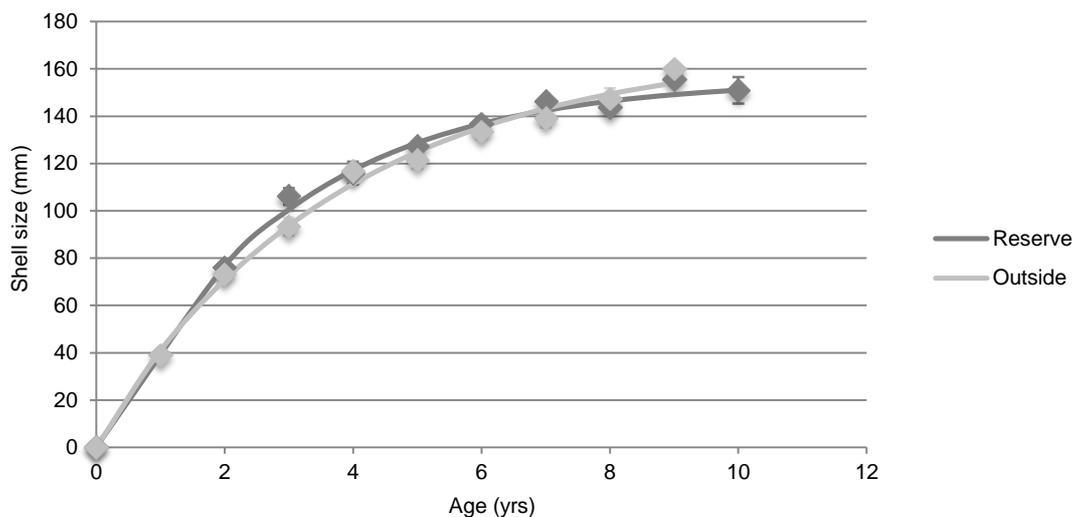

Figure 13. Von Bertalanffy growth curves for *P. maximus* inside and outside the NTZ.

The growth curves fitted to the mean size at age values for *A. opercularis* also revealed a higher rate of approach to theoretical maximum size among the NTZ population (k=0.12, L_∞=172.5, T_0=-0.61) compared to the population outside (k=0.08, L_∞=186.5, T_0=-0.79). These rates were also not comparable as the test of co-incident curves revealed that the two growth models were not significantly different from one another (RSS_ω=10215.69, X_2=5.30, d.f.=3, p=0.15). The growth curves are shown in Fig. 14.
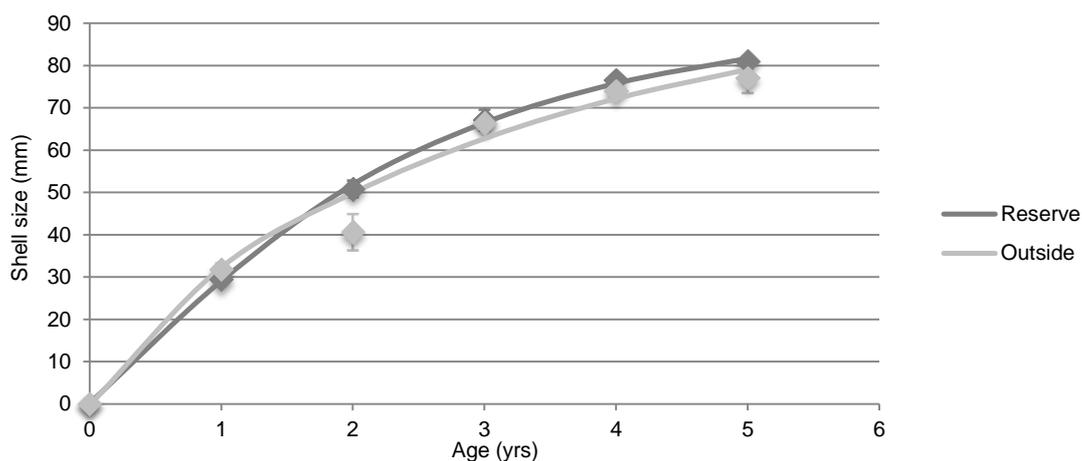
Figure 14. Von Bertalanffy growth curves for *A. opercularis* inside and outside the NTZ.

One way ANOVA comparisons of sub-legal landing size at age *P. maximus* individuals revealed no statistically significant differences between 2 or 3 year old shell sizes inside the NTZ and those outside (Table 7). Sampled 1 year old *A. opercularis* individuals showed no statistically significant difference in size, however significant difference was identified in sizes of 2 year olds; those in the NTZ were 1.25 times larger at age than those outside.

Table 7. One way ANOVA tests of mean size at age in a) 2 and 3 year old *P. maximus* and b) 1 and 2 year old *A . opercularis*. * indicates a significant result.

Scallop age	Mean size at age (reserve)	Mean size at age (outside)	F	p
(a)				
2	76.11 ±3.53	73.18 ±1.46	$0.68_{1,46}$	0.41
3	106.10 ±4.76	93.29 ±3.82	$3.95_{1,25}$	0.06
(b)				
1	29.39 ±0.65	31.83 ±1.48	$1.59_{1,56}$	0.21
2	50.84 ±1.97	40.60 ±4.31	$5.69_{1,27}$	0.02*

4. Discussion

Overall, my study provided inconclusive evidence of the potential scallop fisheries benefits arising from a temperate no take zone. Whilst individuals of both species sampled from the NTZ were larger, older and possessed higher exploitable and reproductive biomass than those from outside, neither species was found to be more abundant. Though earlier studies of the same NTZ drew similar conclusions (Axelsson *et al.,* 2010; Howarth *et al.*, 2011 – although this study did find significantly higher juvenile scallop abundance within the NTZ), recent observations in previous years had identified significantly higher NTZ densities of *P. maximus* in 2011 and 2012 (Howarth, unpublished data).

Clearly, the scale of contrast in scallop densities between fished and unfished zones is related to the intensity of fishing pressure around the edges of the NTZ. Beukers-Stewart et al (2005), for example, found enormous differentials in *P. maximus* densities in the Port Erin closed area, but this zone was subject to much higher original fishing pressure than Lamlash Bay; a pressure that continued after the closed area designation and was concentrated hard up against its boundaries. It is also worth noting that the *P. maximus* densities observed in both Lamlash Bay locales ($6.13/100m^2$ in the NTZ and $5.17/100m^2$ outside) are significantly higher than those observed at Port Erin during the first 9 years of its designation (density increased from an estimated $0.5/100m^2$ in 1989 to $3.5/100m^2$ in 1998).

The similarity of conditions between Lamlash Bay's fished and unfished zones and the homogeneity of their respective scallop populations was also confirmed by the lack of distinction between both species' sets of growth curves. However, the statistical comparison of growth rates between fished and unfished populations carries a high possibility of bias due to the selective, preferential removal of faster-growing individuals from a fished population (Smith, 1994). Indeed, the density-dependence driven response to stock reduction among a fished population can lead to protected populations appearing to exhibit decreased growth rate compared to those outside the boundaries of an MPA; a phenomenon demonstrated among populations of

the rock lobster *Jasus edwardsii* around and within the Maria Island Marine Reserve in Tasmania (Buxton *et al.*, 2006).

Though the effects of spatial protection in ensuring scallop density were not conclusive, my examination of the various environmental variables that were able to predict scallop abundance revealed the importance of structurally complex benthic habitats (the preservation of which is another stated aim of the Lamlash Bay NTZ) in determining distribution. In particular, the association of *P. maximus* with live maerl and hydroid-dominated substrates supports previous studies of this species' habitat preferences, particularly among juveniles (Hall-Spencer *et al.,* 2003; Bradshaw *et al.*, 2003). The strong positive association between *P. maximus* density and that of the seven-armed starfish *Luidia ciliaris* is an apparently anomalous result. Though their co-habitation has been frequently observed in northwestern Scottish and Shetland waters (SNH, 2012), there seems to be little evidence of an ecological relationship between the two species; *P. maximus*, for example, displayed less violent escape reactions under laboratory conditions when exposed to *L. ciliaris* than its known echinoderm predators such as *A. rubens* and *A. irregularis* (Thomas & Gruffydd, 1971).

Similarly, the positive association between *A. opercularis,* the common sunstar *Crossaster papposus* and the bloody Henry starfish *Henricia* spp. appears counter-intuitive, though it is notable that these echinoderm species were found to prosper at the expense of queen scallops in a long-term study of trawling impacts at Strangford Lough, Northern Ireland (Strain *et al.*, 2012); their co-habitation could therefore be tentatively suggested to demonstrate small overall biodiversity increases in the study site, although this assertion cannot be verified. The association with depth is not surprising in this species; *A. opercularis* is anecdotally associated with deeper habitats than *P. maximus* and has been found at depths of up to 100m (Carter, 2009).

Evidently, the effects of strict spatial protection can be obscure when target species appear to exhibit complex and anomalous interactions with their surrounding environment. It is clear that these anomalies could have arisen as

a result of the limited nature of the study, which encompassed only a single year of observation and a highly clustered set of study locations; this last factor undoubtedly also helps to explain the similarity of densities found for both species on either side of the reserve boundaries. Future studies of scallop abundance in the Firth of Clyde should utilise distribution maps of "pings" from >12m scallop dredge vessel monitoring systems (VMS) in order to contrast the protected population with some of the most heavily exploited grounds east of Campbeltown and across southern Arran (McIntyre *et al.*, 2012).

Finally, attention must be drawn to the experimental status of the Lamlash Bay no take zone, especially when contrasted with the suite of restricted and closed areas utilised in the Isle of Man scallop fisheries. The concept of "networked" MPAs – whether subject to full or partial protection from extractive activities – is central to spatial protection plans at global and national levels (CBD, 2010; JNCC, 2013). This logic should be – and has been – applied at hyper-localised level, allowing networks to support and preserve fine-scale ecological linkages whilst reflecting the needs and activities of surrounding communities (Basterretxea *et al.,* 2012; Roberts *et al.,* 2001). For spatial protection measures to be effectively utilised as a fisheries management tool in the Firth of Clyde, replicate closed areas – based on the Lamlash Bay NTZ – must be installed across key pectinid and crustacean fishing grounds in order to ensure that protected pockets of the kind of large, old and fecund individuals identified in this study can support, stabilise and even revive exploited stocks effectively.

Word count: 4,980

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Appendix 1 – Extra-curricular activities

My summer placement was hosted by the Community of Arran Seabed Trust (COAST); the NGO that originally proposed the Lamlash Bay NTZ and continue to play a vital role in enforcing its restrictions. Over the course of the summer I was able to assist the charity with a number of public outreach events, including the 177th Arran Agricultural Show and Brodick tourist centre "meet and greets". My role was two-fold at these events; first, myself and other members of the scientific survey team would complete an extra SCUBA dive a number of hours before the event began and collect a variety of "critters" from outside the NTZ to display in a touch tank. We focussed on species groups such as crustaceans (e.g. *N. puber* and *Pagurus* spp.) and echinoderms (e.g. *A. rubens* and *Echinus esculentus*) that could be returned to the marine environment unscathed afterwards. With the touch tank fully stocked, I would then encourage members of the public to hold the individuals whilst also explaining to them about COAST, the NTZ and the proposed MPA.

Allowing the public this tangible experience of the biodiversity present in UK waters proved to be a highly effective means of disseminating conservation messages and increasing awareness of the topical issues of invasive fishing gear use, spatial protection measures and the importance of localised marine management. There was an infectious enthusiasm among younger members of the public to learn about marine species and many displayed a surprising level of existing knowledge about the subject. I was lucky enough to join in this youthful passion myself at COAST's "Tale of the Whale" event, in which local schoolchildren participated in a craft course in which they made their own moveable cardboard octopus and jellyfish and decorated a large papier-mâché whale. Carrying one side of the whale, I joined in a parade down Lamlash high street and then helped the children take part in a short play about marine litter in which their cardboard creations were props.

Finally, I also took the opportunity to learn from the varied array of scientists, fishermen, conservationists and local divers associated with the charity, all of whom have some sort of stake in the NTZ and proposed MPA. I went out with creel fishermen Charlie Weir aboard his vessel the *Kimberly* to observe his

method of catching *Homarus gammarus*, *C. pagurus* and *Nephrops norvegicus*, also taking the chance to discuss his thoughts on the effects of spatial protection in UK waters. These trips also involved assisting on a separate MSc project on abundance and sizes of these species inside and outside the NTZ; this gave me valuable experience of measuring, sexing and tagging crustaceans. I dived with local underwater photographer and long-time COAST supporter Angus Robson (a dive on which we saw the elusive *Chelidonichthys lucerne* and *Prostheceraeus vittatus* species) who has seen first-hand the seabed recovery associated with the NTZ. I attended presentations from PhD students Sophie Elliott and Joanne Clarke of the University of Glasgow, and discussed with them their respective projects on juvenile gadoid habitat preferences and optimal MPA survey design. Through discussions with COAST chairman Howard Wood and marine project officer Andrew Binnie, I had a privileged insight into the complex administrative processes associated with MPA site designation and the sometimes fractious relationship between governments and localised, community managers.

Overall, the unforgettable experiences, relationships and knowledge I acquired from my summer placement with COAST will undoubtedly prove invaluable in later years and I feel intensely proud of what my colleagues and I achieved.