Article:

Howarth, Leigh Michael, Dubois, Pascal, Gratton, Paul et al. (6 more authors) (2017) Trade-offs in marine protection:Multi-species interactions within a community-led temperate marine reserve. ICES Journal of Marine Science. pp. 263-276. ISSN 1054-3139

https://doi.org/10.1093/icesjms/fsw166

Trade-offs in marine protection: Multi-species interactions within a community-led temperate marine reserve

Leigh M. Howarth[1],[*] Pascal Dubois[2], Paul Gratton[2], Matthew Judge[2], Brian Christie[2], James J. Waggitt[1], Julie P. Hawkins[2], Callum M. Roberts[2] and Bryce D. Stewart[2]

[1]*School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK*
[2]*Environment Department, University of York, Heslington, York, YO10 5DD*

[*]*Corresponding author: tel: +441248 388625, e-mail: l.m.howarth@bangor.ac.uk*

This study investigated the effects of a community-led temperate marine reserve in Lamlash Bay, Firth of Clyde, Scotland, on commercially important populations of European lobster (*Homarus gammarus*), brown crab (*Cancer pagurus*) and velvet swimming crabs (*Necora puber*). Potting surveys conducted over four years revealed significantly higher catch per unit effort (CPUE 109% greater), weight per unit effort (WPUE 189% greater) and carapace length (10-15mm greater) in lobsters within the reserve compared to control sites. However, likely due to low levels of recruitment and increased fishing effort outside the reserve, lobster catches decreased in all areas during the final two years. Nevertheless, catch rates remained higher within the reserve across all years, suggesting the reserve buffered these wider declines. Additionally, lobster CPUE and WPUE declined with increasing distance from the boundaries of the marine reserve, a trend which tag-recapture data suggested to be due to spillover. Catches of berried lobster were also twice as high within the reserve than outside, and the mean potential reproductive output per female was 22.1% greater. It was originally thought that higher densities of lobster within the reserve might lead to greater levels of aggression and physical damage. However, damage levels were solely related to body size, as large lobsters > 110 mm had sustained over 218% more damage than smaller individuals. Interestingly, catches of adult lobsters were inversely correlated with those of juvenile lobsters, and brown and velvet crabs, which may be evidence of competitive displacement and / or predation. Our findings provide evidence that temperate marine reserves can deliver fisheries and conservation benefits, and highlight the importance of investigating multi-species interactions, as the recovery of some species can have knock-on effects on others.

Keywords: marine protected areas, fisheries, ecosystem recovery, ecosystem-based fisheries management, aggression, spillover, competition, larval export

Introduction

The intensity and geographic reach of the world's fisheries has escalated greatly over the last two centuries, causing a dramatic loss of species and fishery resources in virtually every marine ecosystem on Earth (Jackson *et al.*, 2001; Myers and Worm, 2003, 2005; Roberts, 2007; Watson *et al.*, 2013; Howarth *et al.*, 2014). Although many different management measures exist for maintaining and supporting fish stocks, the establishment of Marine Protected Areas (MPAs) closed to some or all types of fishing is considered to be one of the most effective ways to reduce mortality and boost recruitment in fish stocks (Halpern and Warner, 2002; Halpern, 2003; Roberts *et al.*, 2001, 2005; Lester *et al.*, 2009). In doing so, MPAs are regularly reported to increase the abundance of target species, restore size and age structures, enhance reproductive output, and improve the survival and growth of juveniles (Myers *et al.*, 2000; Gaines *et al.*, 2003; Grantham *et al.*, 2003; Beukers-Stewart *et al.*, 2005; Kerwath *et al.*, 2008; Lester *et al.*, 2009; Howarth *et al.*, 2011, 2015b). All of these effects may then result in the greater production of larvae, juveniles and adults which can disperse ("spillover") outside the MPA and contribute to fishery landings (Mcclanahan and Mangi, 2007; Harrison *et al.*, 2012).

If populations are to benefit from the protection afforded by MPAs, it is necessary that a number of individuals spend a substantial part of their lives within their boundaries (Roberts *et al.*, 2005). Lobsters, crabs and other crustaceans have therefore been proposed as ideal species for closed area management thanks to their high value and relatively low mobility (Follesa *et al.*, 2009, 2011; Moland and Olsen, 2011; Moland *et al.*, 2013b). In fact, several studies have found the abundance of lobsters to increase within MPAs 2-25 fold (Shears *et al.*, 2006; Fenberg *et al.*, 2012; Moland *et al.*, 2013a) and that such increases can become evident after just 18 months of protection (Hoskin *et al.*, 2011). Studies also report increases in mean body size (Hoskin *et al.*, 2011; Moland *et al.*, 2013a) and increased catches in neighbouring fishing grounds (Goñi *et al.*, 2006, 2010; Díaz *et al.*, 2011). Then again, other studies suggest MPAs can displace fishing effort to surrounding areas (Bohnsack, 2000; Dinmore *et al.*, 2003; Kaiser, 2005) and that the greater densities of target species within MPAs may lead to greater levels of disease transmission, aggression and physical injury (Wootton *et al.*, 2012; Davies *et al.*, 2014). Also, as MPAs do not address the factors underlying overfishing, many argue that MPAs should be complemented with restrictions on fishing effort and fishing gears, all of which have received mutual consent from fishers and managers (Hilborn, 2007; Worm et al., 2009; Khan and Neis, 2010).

Despite the potential for MPAs to provide fishery benefits, there are currently only three fully protected marine reserves in the United Kingdom (UK) which ban all fishing activity within their boundaries (i.e. are “No-Take Zones” – NTZs). These are Lundy Island, in Devon; Flamborough Head, in North Yorkshire; and Lamlash Bay in the Firth of Clyde. Uniquely, the fully protected marine reserve in Lamlash Bay was established at the request of the local community in September 2008 (Prior, 2011). The efforts made by these local residents were in response to over a century of intensive fisheries exploitation, which led to widespread declines in fisheries and marine wildlife throughout the Firth of Clyde (Thurstan and Roberts, 2010; Howarth *et al.*, 2014). The protected area was therefore passed by Scottish Parliament under the rationale that the reduction in fishing pressure should help regenerate both the local marine environment and enhance commercial shellfish and fish populations in and around Lamlash Bay.

Our study sought to determine if the community-led marine reserve in Lamlash Bay provided benefits to commercially important populations of crabs and lobster. Specifically, we conducted a series of annual potting surveys to test if: (1) catch rates of crab and lobster were higher within the reserve; (2) individuals were larger within the reserve; (3) reproductive potential was greater within the reserve; (4) there was any evidence of spillover from the reserve to surrounding areas; and (5) if increased lobster densities resulted in greater levels of physical damage.

Methods

Scottish crustacean fisheries

Of the three crustacean species in this study, brown crab (*Cancer pagurus*) are the most valuable in Scotland; with total landings in 2013 of around 10,800 tonnes and a first sale value of £13.8 million (Barreto and Bailey, 2015). The fishery has grown substantially over the last four decades and landings have increased fivefold since 1974. Likewise, landings of European lobster (*Homarus gammarus*) have increased three fold since 2001, reaching 1000 tonnes in 2013 (Barreto and Bailey, 2015). Although smaller than the brown crab fishery, lobsters command a higher price per kilogram, which is why they still generated a value of £10.6 million in 2013 (Mill *et al.*, 2009; Mesquita *et al.*, 2013). The fishery for velvet swimming crabs (*Necora puber*) differs in that it is one of the smallest and most recent fisheries in Scotland, and are only fished when prices are high. Hence, only 1600 tonnes of velvet swimming crabs were landed in 2013, worth £4 million (Barreto and Bailey, 2015). All these fisheries are regulated solely by minimum legal landing sizes (Mesquita *et al.*, 2013; Barreto and Bailey, 2015), currently set at 87 mm carapace length for European lobster, 130 mm carapace width for brown crab, and 65 mm for velvet swimming crab. However, concerns have recently been raised over declining recruitment, truncating age structures, failures in egg production and unsustainable levels of fishing mortality in several major crab and lobster stocks around Scotland (Mill *et al.*, 2009; Barreto and Bailey, 2013, 2015; Mesquita *et al.*, 2016).

Sampling design

This study took place around the southern and eastern shores of the Isle of Arran, an island situated off the west coast of Scotland within the Firth of Clyde. Although the marine reserve in Lamlash Bay was established in 2008, no surveys were conducted in the area prior to protection and monitoring of crustacean populations did not begin until 2012. Therefore, as we could not employ a before-after control-impact (BACI) approach (Hilborn *et al.*, 2004; Sale *et al.*, 2005), we monitored crustacean populations within the reserve and in several control areas over a period of four years. This was done on the assumption that a divergence in population characteristics over time would be indicative of an effect (see Howarth *et al.*, 2015a, 2015b).

Sampling occurred along the southern shore of the marine reserve (R1) and at near control sites (N1-N3) as displayed in Figure 1. All sites were on shallow boulder slopes less than 10m in depth and were chosen by an experienced fisherman on the premise that he had caught lobster from those areas in the past. Near control sites were located less than 2.5 km from the reserve's boundaries and were situated to the north, east and west of the reserve. Originally, we intended to sample along both the southern (R1) and northern (R2) shores of the marine reserve. However, a series of SCUBA surveys (Howarth *et al.*, 2011, 2015a, 2015b) indicated that R2 differed markedly from R1 in that the substrate was composed primarily of sandy mud and shell. In addition, not a single lobster was caught in R2 during a pilot potting study in 2012, hence we excluded the area from this study.

Targeted surveys were conducted during one week in mid-July and one week in mid-August for four years between 2012 and 2015. The catchability of crustaceans varies considerably depending on moult stage, reproductive condition, size, sex, seasons, habitats, water temperature and the number of crustaceans already in a trap (Smith and Tremblay, 2003; Jury *et al.*, 2007). Hence, averaging catch rates over the two months was intended to account for any shorter-term fluctuations in catchability. Crustaceans were sampled using standard specification commercial shellfish pots of two-side eye entrance design. Mesh size was 65 mm and pots measured 64 x 38 x 41 cm, with two entrances measuring 21 x 18 cm. Pots were baited with a mix of mackerel (*Scomber scombrus*) and redfish (*Sebastes* spp) and deployed in fleets of five with 20 m between each pot. Marker-buoys were attached to both ends of the fleets, and pots were considered heavy enough to act as their own anchor. For each day of sampling, three fleets were deployed within and outside the reserve parallel to the shore. These were then left to "soak" for approximately 48 hours before being hauled. In 2012, a total of 32 fleets were deployed over the two sampling periods (i.e. 16 in July and 16 in August), half of which were within the reserve and the other within the near control. In 2014 and 2015, this number increased to 36 fleets. However, in 2013, one fleet of pots intended for outside the reserve in July was inadvertently deployed inside. Hence, during this year, 19 sites were sampled within the reserve and 17 outside.

For the years subsequent to 2012, targeted surveys were bolstered with additional fishing observations made aboard two different commercial potting vessels. These took place between July-August within the far control sites (F1-F4) 10-20 km south of the marine reserve. The methods used during these observations differed slightly from the targeted surveys in that fleets varied between 5-10 pots in length and were left to soak between 48-72 hours. While these differences have the potential to inflate catches, it has been observed that when soak times are five days or less, small variations in soak time have no significant effect on the catch rate of lobster (Bennet and Edwards, 1981a; Montogomery, 2005). In addition, our measurements of Catch Per Unit Effort (CPUE) were based upon the average number of individuals caught per pot, negating the impact of varying fleet lengths.

Data collection

The number of individuals of all species captured per pot was recorded. All lobsters, brown crabs and velvet crabs were then measured (to the nearest 1mm) and sexed. Lobsters were measured from behind the eyestalk to the posterior edge of the carapace where the connection with the abdomen is formed. In comparison, crabs were measured at the widest point of their carapace. Signs of biological condition (e.g. eggs, disease and damage) were recorded along with environmental conditions such as the weather, time of day and depth. The geographical coordinates of the capture location were then recorded before individuals were returned to sea in the same capture location. Again, the methodology for the additional fishing observations differed slightly. For these, the number of individuals of all species was recorded, but initially only those individuals above minimum landing size were measured, sexed and inspected for biological condition. Information on undersized individuals began to be recorded from 2014 onwards.

Tagging

All lobsters (2012-2015) and brown crabs (2012 only) caught in this study were marked with a double T-bar anchor tag (Hallprint Pty. Ltd) measuring 55mm in length. These tags were selected for their quick application and high rate of retention during moulting (González-Vicente *et al.*, 2012). Each tag was imprinted with a unique identification number, a telephone number, and coloured either green or orange depending on whether individuals were caught from within or outside the reserve respectively. Tags were inserted using a Monarch Marking 3030 tagging gun. Lobsters were tagged in their abdominal muscle immediately behind the posterior edge of the carapace, either side of the midline, to avoid puncturing the dorsal abdominal artery and the gut (Smith *et al.*, 2001). Brown crabs were tagged where their fourth leg (on either side) joined the rear of the carapace. Geographical coordinates of capture were recorded every time a tagged individual was recaptured either by our potting surveys, or by local fishermen cooperating with this study. Velvet swimming crabs were not tagged due to their small size relative to the tags we had available.

Data analyses – comparisons of CPUE

All analyses treated sites within the fully protected reserve, near control and far control as three independent treatments (i.e. reserve, near control and far control). All variables were tested for normality using histograms, boxplots, QQ plots and the Shapiro–Wilk test within the statistical package R (www.r-project.org). For each species, the mean number of individuals caught per pot was used as an indicator of their CPUE:

$$\text{CPUE} = \frac{\text{Number of individuals caught in fleet}}{\text{Number of pots in fleet}}$$

The CPUE of velvet swimming crabs, brown crabs and lobster were compared among treatments and years using poisson Generalized Linear Models (GLMs). However, initial model runs suggested non-normality and over-dispersion so quasipoisson GLMs were used to overcome this. Diagnostic plots were then used to explore how well the models fitted the data and to identify any extreme outliers. An analysis of deviance utilising Pearson’s Chi-squared test ($\chi 2$) was used to determine which explanatory variables significantly influenced CPUE. The CPUE of the three different crustacean species were also tested for any correlation with each other using Spearman's rank correlation coefficient.

The distance of each sampling location from the boundaries of the marine reserve was calculated using the cost distance tool in ArcGIS 10.2. This method assumed that crustaceans could only travel through the marine environment, and not on land. The mean CPUE of lobsters and brown crabs was then calculated for all sites within the reserve as well as 5 km, 10 km, 15 km and 20 km away. These data were then plotted against distance. Trends between distance and CPUE were tested for significance by using Spearman's rank correlation coefficient. Lastly, a Generalized Additive Model (GAM) was constructed by modelling the mean weekly sea temperature of pot deployment (spline constrained to 3 knots) against lobster CPUE. These data were provided by Marine Scotland (Lynda Blackadder, Marine Scotland, pers. comm.) and collected by an hourly temperature logger located off Great Cumbrae, an island 28 km northeast of Lamlash Bay.

Comparisons of size and weight

The mean size of lobsters and crabs sampled across all four years were compared among treatments using a one-way ANOVA. In addition, their overall size distributions were compared among treatments using a Kolmogorov-Smirnov (K-S) two sample test. Data from the far control were used whenever possible. The weight of lobsters was estimated for males and females separately by applying length-weight relationships inferred from Leslie *et al.* (2006):

$$\text{Weight of male lobster (g)} = 0.0022 \times \text{length}^{2.7416}$$

$$\text{Weight of female lobster (g)} = 0.0016 \times \text{length}^{2.8134}$$

In order to explore the weight of lobster caught per pot, Weight Per Unit Effort (WPUE) was calculated using the following equation:

$$\text{WPUE (g)} = \frac{\text{Total weight of lobster in fleet}}{\text{Number of pots in fleet}}$$

As with CPUE, the WPUE of lobsters was compared among treatments and years using quasipoisson GLMs. The mean WPUE of lobsters was also calculated for all sites within the reserve, as well as 0.5 km, 1 km, and 1.5 km away. These data were then plotted against distance. Trends between distance and WPUE were tested for significance by calculating Spearman's rank correlation coefficient. Distances greater than 1.5 km could not be used as these data were collected from the far control where data on undersized individuals had been recorded inconsistently.

Comparisons of gender ratios and fecundity

A Pearson Chi-squared test was used to determine if the frequency of male and female lobsters differed from an equal sex ratio. The same test was also used to investigate whether the frequency of male and female lobsters significantly differed between the reserve and near control sites over time. Lastly, the same test also helped determine if the frequency of berried and non-berried females differed from the reserve and near control sites. Similar to the calculations of WPUE, the potential reproductive output of each female lobster caught was estimated using fecundity-length relationships of Lizárraga-Cubedo *et al.* (2003):

$$\text{Potential reproductive output} = (1.554 \times \text{length}) - 10286$$
$$\text{(number of eggs per female)}$$

The potential reproductive output per female lobster was then compared between the reserve and near control for both years using a Mann–Whitney–Wilcoxon test. Data collected from the far control could not be used for reasons already explained.

Comparisons of damage

The level of damage sustained by each lobster was calculated by assigning every individual a score using the following system: damaged / regrown limb or antenna = 1; missing limb or antenna = 2; damaged / regrown claw = 2; missing claw = 4; damage to body = 8. Our intention was to assign higher scores for greater levels of damage that had recently occurred (i.e. a missing claw was worth more than a claw that had regrown). A score of 36 was the most damaged a living lobster could be as this would have all limbs, claws and antennae missing and a damaged core. Scores were then converted to a percentage by:

$$\text{Damage (\%)} = \frac{\text{Damage (score)}}{36} \times 100$$

Damage was then modelled against lobster CPUE, size and treatment using a quasipoisson GLM as previously described

Results

Catch rates

All three commercially important crustacean species displayed significant differences in CPUE between treatments and years (Table 1). In detail, the CPUE of lobster did not differ between the reserve and near control during the first year of study (Figure 2). However, surveys conducted the following year saw the CPUE of lobster within the reserve increase 27% to 1.65 (±0.11 SE) and decrease in the near control 6% to 1.23 (±0.14 SE), a difference of 34.2%. For the final two years of study, both the reserve and near control underwent a 23% decline in lobster CPUE, whereas the far control only declined by 11%. These variations in CPUE were more pronounced when only lobsters of legal landing size were considered. In 2012, the mean CPUE of legal sized lobster was 0.83 (±0.15 SE) and 0.73 (±0.18 SE) within the reserve and near control respectively. Again, surveys conducted in 2013 saw the CPUE of lobster within the reserve increase 32% to 1.1 (±0.09 SE) and decrease in the near control by 31% to 0.5 (±0.1 SE), meaning CPUE was 123% greater inside the closed area. Similar to before, the CPUE of legal lobster declined during the final two years of study across all treatments. Interestingly, this decline only resulted in CPUE of legal lobsters in reserve in 2015 returning to 2012 levels (0.81 compared to 0.83), whereas outside the reserve it dropped to less than half of 2012 levels (0.3 compared to 0.73). The CPUE of sub-legal lobsters differed in that catch rates averaged 37% lower within the reserve compared to both controls, but still exhibited a general decline similar to the other size classes of lobster. Overall, weekly mean sea temperatures exhibited a general decline of 0.75˚C

(±0.03 SE) over the four year study period. However, this variation in temperature had not significantly influenced catch rates of lobster (GAM; Deviance = 3.1%; $\chi^2 = 263.2$; $P > 0.05$).

In contrast to lobsters, catch rates of brown crab were consistently greater (15-115%) within the control treatments than the marine reserve for all years of study. The CPUE of brown crabs was very similar within (0.28 ±0.01 SE) and outside the reserve (0.33 ±0.01 SE) for the first year of study. However, in 2013, CPUE had decreased within the reserve by 49% to 0.15 (±0.04 SE) and increased in the near control by 63% to 0.53 (±0.15 SE), a difference of 253%. Unlike lobsters, the CPUE of brown crab increased 130% during the final two years across all treatments. Catch rates of legal sized brown crab showed similar trends.

Compared to the other two species, the CPUE of velvet swimming crabs fluctuated strongly from year to year within the reserve. For example, CPUE declined 90% in 2013, then increased 176% in 2014, before declining again in 2015 by 72%. Nonetheless, catch rates were higher within in the reserve than both controls for all years except 2013. In contrast, the CPUE of velvet crabs showed a slight increase each year within the controls. Hence, both protection and year were found to have significantly influenced catch rates of velvet swimming crabs.

Crustacean catch rates also displayed strong spatial trends (Figure 3) as the CPUE of legal sized lobsters significantly declined with increasing distance from the boundaries of the fully protected marine reserve (Spearman's rank; $N = 380$; $R = -0.34$; $P < 0.001$). In fact, catches of legal sized lobster were over twice as high within the reserve compared to sites located 5, 10, 15 and 20 km away from the reserve's boundaries. In contrast, the CPUE of undersized lobster was two times lower within the reserve than sites located 20 km away (Spearman's rank; $N = 380$; $\mathrm{R} = 0.23$; $P < 0.001$). Likewise, both the CPUE of brown crab (Spearman's rank; $N = 380$; $R = 0.38$; $P < 0.001$) and undersized brown crab (Spearman's rank; $N = 380$; $\mathrm{R} = 0.39$; $P < 0.001$) were also found to increase with distance from the reserve.

The catch rates of some crustacean species also displayed significant interactions with the catch rates of others. For example, catch rates of lobster and brown crabs were significantly negatively correlated (Spearman's rank; $N = 380$; $R = -0.35$; $P < 0.001$) as was the CPUE of lobsters and velvet swimming crabs (Spearman's rank; $N = 380$; $R = -0.2$; $P < 0.001$). In contrast, the CPUE of brown crabs and velvet swimming crabs were positively correlated (Spearman's rank; $N = 380$; $R = 0.12$; $P = 0.02$).

Lobster movements and growth

A total of 832 lobsters and 68 brown crabs were tagged during the four year study period. No brown crabs were ever recaptured, which is why tagging of crabs stopped after 2013. However, 78 lobsters were recaptured, generating a recapture rate of 9.4%. Of these recaptures, three individuals had moved from within the reserve to outside, and four had moved from outside the reserve to inside. All of the others were recaptured in the same zone they were tagged. On average, recaptured lobsters had travelled a mean distance of 0.66km (±0.12 SE) from tagging sites and increased in carapace length by 0.89 mm per month (±0.07 SE).

Size and weight distributions

The mean size of lobsters was 10 and 15 mm greater (ANOVA, $F_{(2,869)} = 23.8$, $P < 0.001$) within the reserve compared to near and far control sites respectively (Figure 4). Likewise, velvet swimming crabs were 2mm larger within the reserve than both controls (ANOVA, $F_{(1,159)} = 4.2$, $P < 0.05$). In contrast, brown crabs were 25 mm larger within the near control compared to the marine reserve (ANOVA, $F_{(1,171)} = 14.3$, $P < 0.05$).

Comparing the overall size distribution of crustaceans also revealed differences among treatments. Lobster populations within the marine reserve were composed of larger individuals for all years of study (Table 2). In fact, large lobsters >111 mm were entirely absent in the near and far controls (Figure 5). Likewise, large velvet swimming crabs >80 mm were absent in the near control. However, significant differences among treatments only occurred in 2014 and 2015 when sample sizes of velvet crabs were much higher. During these two years, velvet crabs displayed a peak size of 71-75 mm within the reserve compared to 61-65 mm in the near control. Similarly, brown crabs only exhibited a significant difference among treatments in 2015, when sample sizes for this species were also much greater. In this year, the size of brown crabs peaked at 91-100 mm within the reserve but peaked substantially higher at 161-170 mm within the near control.

Differences in the weight of lobster caught per pot were also observed between treatments (Figure 6). These were initially minor during the first year of study but by 2015 the average fleet of 5 pots set inside the reserve yielded 3.5 kg of lobster (SE ± 0.03) compared to just 1.5 kg (SE ± 0.05) outside the reserve; a significant difference of 133% (Table 3). Similar to CPUE, these differences in WPUE were more pronounced for lobsters of legal landing size which were 233% higher within the reserve compared to outside. Again, as was observed with CPUE, the WPUE of lobster increased 26% within the reserve and decreased 11% outside between 2012 and 2013, before experiencing a 27% decline for the final two years of study across all treatments. Like before, the WPUE of all lobsters (Spearman's rank; $N = 140$; $R = -0.42$; $P < 0.001$) and legal sized lobsters (Spearman's rank; $N = 140$; $R = -0.45$; $P < 0.001$) significantly declined with increasing distance from the boundaries of the fully protected marine reserve (Figure 7) as pots set within the reserve yielded 100% more lobster biomass compared to pots set 1, 1.5 and 2 km away.

Damage and disease

Statistical analyses of shell disease and damage levels were difficult due to very low occurrences of both. In terms of disease, only 18 lobsters (out of 2449 = 0.73%) and 20 brown crabs (out of 1113 = 1.8%) displayed any sign of disease across the entire study period. Similarly, only 36 brown crabs (3.23%) showed signs of damage. However, 114 lobsters (4.6%) were damaged which allowed for statistical analysis. Damage in lobsters ranged from 0% (no damage) to 44.4% (individual missing 1 claw and 6 legs). Mean damage scores for lobsters located within the marine reserve were 1.9 times higher than for those located outside. The combination of higher lobster catches (potentially correlated with competition) and levels of damage within the reserve, suggested that greater lobster CPUE resulted in more damage. However, a GLM revealed that the level of damage an individual had sustained was solely related to its size (Table 4). In fact, large lobsters > 110 mm had sustained over 218% more damage than smaller individuals irrespective of whether they were sampled from within or outside the reserve (Figure 8).

Lobster gender ratios and fecundity

Catches of male lobster were higher than females in all treatments across all years (Table 5). However, comparisons among treatments revealed that there was no difference in the frequency of male and female lobsters between the reserve and near control (Table 6). More than twice as many berried lobsters were caught within the reserve than the near control for every year of study, yet 2015 was the only year where this difference was significant (Table 7). Nonetheless, the mean potential reproductive output per female lobster was 22.1% greater within the reserve than outside (Mann-Whitney: $U = 8075$, $N = 296$, $P < 0.001$). Overall, the total reproductive output (i.e. the sum of the reproductive potential of each female lobster) was 70% greater than the near control, equivalent to 46,000 more eggs within the areas sampled.

Discussion

This study provides evidence that, after nearly seven years of protection, the fully protected marine reserve in Lamlash Bay is benefitting commercially important populations of European lobster by increasing their catches, body size and reproductive output. Furthermore, as lobsters are migrating from within the reserve to outside, these benefits are likely being transferred to neighbouring fishing grounds. Then again, the greater densities of large adult lobsters (inferred from higher catch rates) appear to be predating and / or competitively displacing juvenile lobsters, brown crabs and velvet swimming crabs from the area. Combined with our previous work at this location (see Howarth *et al.*, 2011, 2015a, 2015b), this study provides further evidence that temperate marine reserves can deliver fisheries and conservation benefits, but that recovery is not straight forward, as the recovery of some species can have knock-on effects on others.

Consistent with other MPA studies (Hoskin *et al.*, 2011; Moland *et al.*, 2013a), lobsters were significantly larger within Lamlash Bay marine reserve compared to neighbouring fishing grounds across all four years of study. In fact, large lobsters greater than 111 mm were entirely absent outside the reserve, meaning individuals were on average 10-15 mm larger within the reserve than control sites. As egg production is a function of body size and maturity, the greater abundance of large bodied lobsters should translate to higher reproductive output and recruitment both within the reserve and surrounding areas (Beukers-Stewart *et al.*, 2005; Goñi *et al.*, 2008; Cudney-Bueno *et al.*, 2009; Planes *et al.*, 2009; Pelc *et al.*, 2010; Harrison *et al.*, 2012;). In support of this, the mean potential number of eggs per female lobster was 22.1% higher within the reserve than outside, and the total number of eggs was 70% higher, equivalent to 46,000 more eggs within the areas sampled. Additionally, catch rates of berried lobsters were twice as high within the reserve as outside. Together, these results support the hypothesis that individuals located within protected areas experience increased survivorship, allowing for increased body size and reproductive output.

Catch rates of berried lobster were twice as high within the reserve as outside. If there was a greater proportion of females within the reserve this trend would have been easily explained, as more females should equate to more berried females. However, as we observed no difference in sex ratios between the reserve and outside, it is more likely a consequence of lobsters being larger within the closed area. To explain, female lobsters reach sexual maturity at approximately 77 mm in size, or 4-12 years old in age (Simpson, 1961; Barreto and Bailey, 2015). As catch rates of large-bodied adults were lower outside the reserve it is likely that sexually mature, berried female lobsters were less abundant. Added to this, berried female lobsters exhibit less mobility and therefore lower catchability than non-berried females (Agnalt *et al.*, 2007) further lowering the probability of catching berried lobsters outside the reserve. Interestingly, this study caught significantly more males than females. However, government reports indicate male and female lobsters are generally landed in equal proportions in Scotland (Mill *et al.*, 2009). Again, this could be explained by the lower catchability of berried lobsters which would reduce the number of females caught both within and outside the reserve. Whichever the reason, it has been legal to land berried lobsters in the UK since 1966 (Bennet and Edwards, 1981b), meaning the marine reserve should act as a safe haven for sexually mature lobsters, allowing them to contribute to recruitment.

Consistent with the increases in body size and fecundity, overall catch rates of lobster were 109% higher within the reserve than the near control during the final year of study. When only lobsters of legal landing size were considered, this difference was 146%, reflecting the higher catch rates of large lobster within the protected area. Similar differences were also observed between the reserve and control sites located 20 km away, suggesting these differences were not just constrained to areas located directly outside reserve boundaries. Because of these differences, the average fleet of pots set within the marine reserve yielded 2.5 kg more lobster compared to outside, a difference of 133%. Again, these differences were greater for lobsters of legal landing size, which generated 233% higher yields within the reserve.

Although lobster catches have increased within the reserve compared to surrounding areas, they have not followed a clear upward trajectory. When our surveys began in 2012, there was almost no difference in CPUE between the reserve and near control. However, lobster catches increased within the reserve during the following year. Lobster catch rates either then stabilised or declined across all treatments for the final two years of study. Importantly, the marine reserve appears to have buffered wider declines as positive differences between the reserve and surrounding fishing grounds were maintained, and in some cases increased, during this period. But the question remains, why did lobster CPUE decrease between 2014 and 2015, and why would these declines affect those lobsters within the marine reserve? An obvious explanation would be that lobster stocks within the Firth of Clyde are under intensive fishing pressure. Between 2009 and 2012 (the latest available assessment) both males and females were reported as being fished above Maximum Sustainable Yield (MSY; Mesquita *et al.*, 2016). There have also been reports of increased fishing activity along the boundaries of the reserve over the last four years (Andrew Binnie, COAST, personal observation). Added to this, catches of undersized lobsters declined between 2012 and 2015, suggesting very little recruitment had occurred during this period. Together, this evidence suggests that increasingly high numbers of lobster were being removed through fishing and not being replaced by recruitment. As lobsters from within the reserve were spilling over to neighbouring fishing grounds, they too were capable of being taken by the fishery. This may explain why CPUE declined both within and outside the reserve.

Despite our positive results, the 109% difference in lobster CPUE between Lamlash Bay marine reserve and surrounding areas is less than those documented by other MPA studies. In the Lundy MPA, which is only slightly larger than the one in Lamlash Bay, the CPUE of European lobsters was 171% higher within the reserve than control sites after just four years of protection (Hoskin *et al.*, 2011). Likewise, several MPAs off the coast of Norway, all similar in size to Lamlash Bay, increased lobster CPUE by 245%, again after just four years of protection (Moland *et al.*, 2013a). Along with the factors discussed above, it is likely that limited amounts of suitable lobster habitat in the Lamlash reserve may be responsible for the smaller differences in our study. Previous surveys in the area (Howarth *et al.*, 2011, 2015a, 2015b) revealed that the rocky and boulder habitats preferred by lobsters (Mehrtens *et al.*, 2005; Mill *et al.*, 2009; Barreto and Bailey, 2015) are only present along the southern edge of the reserve. This could be reducing the amount of area within the reserve available for lobster habitation, which would limit the extent of any benefits the fully protected marine reserve can bestow on lobsters. This highlights that marine reserves must be well designed to maximise their effectiveness; incorporating suitable habitat and being of adequate size to protect species of interest (see Edgar *et al.*, 2014). For brown crabs, their high mobility and extensive seasonal migrations to offshore spawning grounds (Bennett and Brown, 1983) is likely to constrain any benefits they may receive from protection. Consequently, the small size of Lamlash Bay marine reserve may, at best, only provide protection during a very limited part of their annual range. Much larger protected areas encompassing aggregation sites or spawning areas would probably be necessary if closed areas were to be of any benefit to this species (Ungfors *et al.*, 2007). In contrast to brown crabs, the movements of velvet crabs are thought to be restricted to a few hundred metres (Baretto and Bailey, 2015). Although this makes them an ideal candidate for protection, stocks are only seasonally/ lightly exploited, meaning their response to protection will also likely be limited.

Higher densities of target organisms can lead to greater levels of disease transmission and physical injury (Davies *et al.*, 2014; Howarth *et al.*, 2014). For example, both Wooton et al., (2012) and Davies et al., (2014) found higher damage rates in large lobsters in Lundy MPA, and highlighted this as a potentially negative effect of marine reserves. This is because lobsters are solitary, territorial animals and are well known to fight each other when in close proximity (Debuse *et al.*, 1999; Williams *et al.*, 2006). Given the higher abundance of lobsters within Lamlash bay, we too expected lobsters within the closed area to show higher levels of damage. Consistent with this, lobsters located within the Lamlash Bay marine reserve were 1.9 times more damaged than those outside However, unlike what was observed in Lundy, a GLM revealed that the level of damage an individual had sustained was solely related to its body size, and not CPUE as expected. In fact, large lobsters greater than 110 mm had sustained over 218% more damage compared to smaller individuals, regardless of whether they were captured within or outside the reserve. This trend may be explained by four combining factors: (1) large lobsters are usually stronger, have a greater ability to inflict injury, and are therefore more likely to win a fight (Karnofsky *et al*., 1989; Thorpe *et al.*, 1994; Huber and Kravitz, 1995; Huber *et al.*, 1997; Arnott and Elwood, 2009); (2) lobsters that win a fight are more likely to win a subsequent one, and are therefore less likely to stand down from a fight (Huber *et al.*, 1997); (3) larger individuals would be older, and therefore would have had more opportunities to become subject to attack and injury than smaller individuals; and (4) larger lobsters moult less frequently than smaller ones, hence accumulated damage may be slower to repair in large individuals (Hughes and Matthiesen, 1962). Overall though, we observed much lower levels of damage compared to the MPA in Lundy (4.65 % compared to 33 %) and almost no disease (0.73% compared to 24%; Davies *et al.*, 2014).

An effective way for lobsters to avoid fights and intraspecific competition would be to move outside the boundaries of the reserve where lobster densities are lower. Additionally, as the abundance of large lobsters was greater within the reserve, we would also expect a greater proportion of juvenile lobsters to be displaced by territorial disputes, meaning both lobster size and abundance should decrease with increasing distance from the reserve (Follesa *et al.*, 2009). In support of these two theories, both lobster CPUE and WPUE significantly declined with increasing distance from the reserve. Models and empirical evidence suggest that such declining trends are likely to be evidence of spillover (Kellner *et al.*, 2007). In support of this, data from our tagging study confirmed that spillover had occurred in Lamlash Bay, as has been observed for lobsters in several other studies of MPAs (Goñi *et al.*, 2006, 2010; Díaz *et al.*, 2011;).

It is likely that aggressive and competitive interactions also occurred between lobsters and crabs as adult lobsters are known to predate on smaller crustaceans and compete aggressively with larger individuals for food (Cobb and Castro, 2006; Williams *et al.*, 2006). In support of this, catch rates of lobster and crabs were inversely correlated; meaning years of high lobster CPUE coincided with low catches of brown crabs and velvet swimming crabs, and vice versa. An alternative explanation is that these trends are an artefact of the sampling method. In locations where pots caught high numbers of lobster, fear of predation may have reduced velvet and brown crabs' willingness to enter pots and/or made them more likely to exit if already inside (Hoskin *et al.*, 2011). Either response would result in a false appearance of declining abundance of crabs in areas with high abundance of lobsters. However, this is unlikely as lobster and crabs were frequently caught in the same pot, and showed no evidence of predation between the two (although there was evidence of fighting between lobsters). There is also a possibility that lobsters and brown crabs predate on velvet swimming crabs, as catches of velvet crabs were highest in 2014 when catches of both lobster and brown crab were low. However, despite the potential negative effects of high lobster and brown crab densities on velvet swimming crabs, the CPUE and size of velvet crabs remained higher within the reserve for most years of our study, suggesting that competition / predation between velvet crabs and lobster may be weaker than for brown crabs.

Following a large number of recently established policies and initiatives, the global coverage of MPAs is set to increase dramatically over the next decade (Wood *et al.*, 2008; CBD, 2011; Harrop, 2011; Wood, 2011; Fenberg *et al.*, 2012; Jones, 2012; Metcalfe *et al.*, 2013; JNCC, 2016;). However, studies into the effects of MPAs remain relatively scarce in temperate and cold waters, and are particularly limited in Europe and the UK (Fenberg *et al.*, 2012). Out of the few that do exist, the majority have investigated changes in specific ecological or fishery components, rather than investigating the ecosystem as a whole, either focusing solely on benthic habitats (e.g. Sheehan *et al.*, 2013) or just one or two species of commercial importance (Beukers-Stewart *et al.*, 2005; Hoskin *et al.*, 2011; Moland *et al.*, 2013a). However, our research within Lamlash Bay (this study and Howarth *et al.*, 2011, 2015a, 2015b) has shown that a wide range of species and habitats can benefit from protection, but far from all. Hence, our work highlights that it is far more valuable to study as many components of the ecosystem as possible, rather than one alone. This study also highlights marine reserves must be well designed if they are to be of benefit to the species they intend to protect. The small size of Lamlash Bay marine reserve offers little benefit to brown crabs, and the lack of suitable habitat probably caps benefits to lobsters. For reasons such as these, it is unlikely that small MPAs alone (such as Lamlash Bay) will be enough to counter the high levels of fishing mortality and low levels of recruitment currently being reported in several major crab and lobster stocks around Scotland (Tully *et al.*, 2001; Mill *et al.*, 2009; Barreto and Bailey, 2013, 2015; Mesquita *et al.*, 2016;). At present, shellfish fisheries within the Firth of Clyde are only managed through minimum legal landing size. However, it is widely agreed that a combination of managing fishing effort, fishing gears and establishing protected areas, all of which have received mutual consent from managers, fishermen and other stakeholders, is by far the most effective way to restore stocks and marine ecosystems (Hilborn, 2007; Worm *et al.*, 2009; Khan and Neis, 2010;).

Acknowledgments

This study was funded by Fauna and Flora International, the Kilfinan Trust, and the Community of Arran Seabed Trust (COAST) to whom we are very grateful. Likewise, we thank the many people who have helped support this project over the years, particularly to Ocean Breeze Rib Tours and COAST for providing logistical support. Special thanks to Charlie Weir, Tim James and Iain Cossack for all their expertise and assistance in the field. Thank you also to Lynda Blackadder, Marine Scotland, for providing us with temperature data from the Millport Biological station. Finally, thanks to Eamon Murphy and Heather Tibbetts, Marine Scotland, for providing the derogation permits which allowed for experimental catch and release fishing with the Lamlash Bay marine reserve.

References

Agnalt, A. L., Kristiansen, T. S., and Jørstad, K. E. 2007. Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway. ICES Journal of Marine Science, 64: 288–297.

Arnott, G., and Elwood, R. W. 2009. Assessment of fighting ability in animal contests. Animal Behaviour, 77: 991–1004.

Barreto, E., and Bailey, N. 2013. Fish and shellfish stocks: 2013 edition. Marine Scotland Science, Aberdeen. 1-65 pp. http://www.scotland.gov.uk/Publications/2013.

Barreto, E., and Bailey, N. 2015. Fish and shellfish stocks: 2015 Edition. Marine Scotland Science, Aberdeen. 1-58 pp. http://www.gov.scot/Resource/0047/00477088.pdf.

Bennet, D., and Brown, C. (1983) Crab (*Cancer pagurus*) migrations in the English Channel. Journal of the Marine Biological Association of the United Kingdom, 63: 371-398.

Bennet, D., and Edwards, E. 1981a. The effects of pot immersion time on catches of lobsters, *Homarus gammarus* (L.) in the Welsh coast fishery. Technical Report 36: 1–4. CEFAS, Lowestoft.

Bennet, D., and Edwards, E. 1981b. Should we ban the berried lobsters? ICES Document CM 1981/K: 11. ICES, Copehagen, Denmark.

Beukers-Stewart, B. D., Vause, B. J., Mosley, M. W. J., Rossetti, H. L., and Brand, A. R. 2005. Benefits of closed area protection for a population of scallops. Marine Ecology Progress Series, 298: 189–204.

Bohnsack, J. A. 2000. A comparison of the short-term impact of no-take marine reserves and minimum size limits. Bulletin of Marine Science, 66: 635–650.

CBD. 2011. Diversity, Report of the 10th meeting of the conference of the parties to the Convention on Biological. Nagoya, Japan.

Cobb, J., and Castro, K. 2006. *Homarus* species. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, pp. 310–339. Ed. by B. Phillips. Blackwell Publishing ltd, Oxford.

Cudney-Bueno, R., Lavin, M. F., Marinone, S. G., Raimondi, P. T., and Shaw, W. W. 2009. Rapid effects of marine reserves via larval dispersal. PLoS ONE, 4: e4140.

Davies, C. E., Johnson, A. F., Wootton, E. C., Greenwood, S. J., Clark, K. F., Vogan, C. L., and Rowley, A. F. 2014. Effects of population density and body size on disease ecology of the European lobster in a temperate marine conservation zone. ICES Journal of Marine Science, DOI: 10.1093/icesjms/fsu237

Debuse, V., Addison, J., and Reynolds, J. 1999. The effects of sex ratio on sexual competition in the European lobster. Animal behaviour, 58: 973–981.

Díaz, D., Mallol, S., Parma, A., and Goñi, R. 2011. Decadal trend in lobster reproductive output from a temperate marine protected area. Marine Ecology Progress Series, 433: 149–157.

Dinmore, T. A., Duplisea, D. E., Rackham, B. D., Maxwell, D. L., and Jennings, S. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES Journal of Marine Science, 60: 371–380.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., *et al.* 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature, 506: 216–20.

Fenberg, P. B., Caselle, J. E., Claudet, J., Clemence, M., Gaines, S. D., Antonio Garcia-Charton, J., Goncalves, E. J., *et al.* 2012. The science of European marine reserves: Status, efficacy, and future needs. Marine Policy, 36: 1012–1021.

Follesa, M. C., Cannas, A., Cau, D., Cuccu, A., Gastoni, A., Ortu, A., Pedoni, C., *et al.* 2011. Spillover effects of a Mediterranean marine protected area on the European spiny lobster *Palinurus elephas* (Fabricius, 1787) resource. Aquatic Conservation: Marine and Freshwater Ecosystems, 21: 564–572.

Follesa, M. C., Cuccu, R., Cannas, A., Sabatini, A., Deianna, A., and Cau, A. 2009. Movement patterns of the spiny lobster *Palinurus elephas* (Fabricius, 1787) from a central western Mediterranean protected area. Scientia Marina, 73: 499–506.

Gaines, S. D., Gaylord, B., and Largier, J. L. 2003. Avoiding Current Oversights in Marine Reserve Design. Ecological Applications, 13: S32–S46.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., Polti, S., *et al.* 2008. Spillover from six western Mediterranean marine protected areas: Evidence from artisanal fisheries. Marine Ecology Progress Series, 366: 159–174.

Goñi, R., Hillborn, R., Díaz, D., Mallol, S., and Alderstein, S. 2010. Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series, 400: 233–243.

Goñi, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny Lobsters *Palinurus Elephas* from a marine reserve to an adjoining fishery. Marine Ecology Progress Series, 308: 207–219.

González-Vicente, L., Díaz, D., Mallol, S., and Goñi, R. 2012. Tag loss in the lobster *Palinurus elephas* (Fabricius, 1787) and implications for population assessment with capture-mark-recapture methods. Fisheries Research, 129–130: 1–7.

Grantham, B. A., Eckert, G. L., and Shanks, A. L. 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecological Applications, 13: 108–116.

Halpern, B. S. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications, 13: S117–S137.

Halpern, B. S., and Warner, R. R. 2002. Marine reserves have rapid and lasting effects. Ecology Letters, 5: 361–366.

Harrison, H. B., Williamson, D. H., Evans, R. D., Almany, G. R., Thorrold, S. R., Russ, G. R., Feldheim, K. A., *et al.* 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Current Biology, 22: 1023–1028.

Harrop, S. R. 2011. 'Living In Harmony With Nature'? Outcomes of the 2010 Nagoya Conference of the Convention on Biological Diversity. Journal of Environmental Law, 23: 117–128.

Hilborn, R. 2007. Moving to sustainability by learning from successful fisheries. Ambio, 36: 296–303.

Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., *et al.* 2004. When can marine reserves improve fisheries management? Ocean and Coastal Management, 47: 197–205.

Hoskin, M. G., Coleman, R. A., von Carlshausen, E., and Davis, C. M. 2011. Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. Canadian Journal of Fisheries and Aquatic Sciences, 68: 185–200.

Howarth, L. M., Pickup, S. E., Evans, L. E., Cross, T. J., Hawkins, J. P., Roberts, C. M., and Stewart, B. D. 2015a. Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. Marine Environmental Research, 107: 8–23.

Howarth, L. M., Roberts, C. M., Hawkins, J. P., Steadman, D. J., and Beukers-Stewart, B. D. 2015b. Effects of ecosystem protection on scallop populations within a community-led temperate marine reserve. Marine Biology, 162: 823–840.

Howarth, L. M., Roberts, C. M., Thurstan, R. H., and Stewart, B. D. 2014. The unintended consequences of simplifying the sea: Making the case for complexity. Fish and Fisheries, 15: 690–711.

Howarth, L. M., Wood, H. L., Turner, A. P., and Beukers-Stewart, B. D. 2011. Complex habitat boosts scallop recruitment in a fully protected marine reserve. Marine Biology, 158: 1767–1780.

Huber, R., and Kravitz, E. A. 1995. A Quantitative-Analysis of agonistic behavior in juvenile American lobsters (*Homarus Americanus*). Brain Behavior and Evolution, 46: 72–83.

Huber, R., Smith, K., Delago, A., Isaksson, K., and Kravitz, E. A. 1997. Serotonin and aggressive motivation in crustaceans: altering the decision to retreat. Proceedings of the National Academy of Sciences of the United States of America, 94: 5939–5942.

Hughes, J.T. and Matthiesen, G.C. (1962) Observations on the biology of the American lobster, *Homarus americanus*. Limnology and Oceanography, 7:414-421.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., *et al.* 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science, 293: 629–637.

JNCC. 2016. UK Protected Sites. http://jncc.defra.gov.uk/default.aspx?page=4 (last accessed 24 May 2016).

Jones, P. J. S. 2012. Marine protected areas in the UK: challenges in combining top-down and bottom-up approaches to governance. Environmental Conservation, 39: 248–258.

Jury, S., Howell, H., O'Grady, D., and Watson, W. 2007. Lobster trap video: in situ video surveillance of the behaviour of *Homarus americanus* in and around traps. Marine and Freshwater Research, 52: 1125–1132.

Kaiser, M. J. 2005. Are marine protected areas a red herring or fisheries panacea? Canadian Journal of Fisheries and Aquatic Sciences, 62: 1194–1199.

Karnofsky, E.B., Atema, J. and Elgin, R.H. (1989) Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. Biology Bulletin, 176: 239-246.

Kellner, J., Tetreault, I., Gaines, S. D., and Nisbet, R. M. 2007. Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications, 17: 1039–1054.

Kerwath, S. E., Götz, A., Attwood, C. G., and Sauer, W. H. H. 2008. The effect of marine protected areas on an exploited population of sex-changing temperate reef fish: an individual-based model. African Journal of Marine Science, 30: 337–350.

Khan, A. S., and Neis, B. 2010. The rebuilding imperative in fisheries: Clumsy solutions for a wicked problem? Progress in Oceanography, 87: 347–356.

Leslie, B., Henderson, S., and Riley, D. 2006. Lobster stock conservation: V-Notching. Fisheries Development Note No. 22. NAFC Marine Centre. Scalloway, Shetland. 4 pp.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airame, S., *et al.* 2009. Biological effects within no-take marine reserves: A global synthesis. Marine Ecology Progress Series, 384: 33–46.

Lizárraga-Cubedo, H. A., Tuck, I., Bailey, N., Pierce, G., and Kinnear, J. A. 2003. Comparisons of size at maturity of two Scottish populations of the European lobster, *Homarus gammarus*. Fisheries Research, 65: 137–152.

Mcclanahan, T. R., and Mangi, S. 2007. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecological Applications, 10: 1792–1805.

Mehrtens, F., Stolpmann, M., Buchholz, F., Hagen, W., and Saborowski, R. 2005. Locomotory activity and exploration behaviour of juvenile European lobsters (*Homarus gammarus*) in the laboratory. Marine and Freshwater Behaviour and Physiology, 38: 105–116.

Mesquita, C., Dobby, H., and Mclay, A. 2013. Crab and Lobster Fisheries in Scotland: Results of Stock Assessments 2009 – 2012: Scottish Marine and Freshwater Science Vol 7 No 9. Marine Scotland Science, Edinburgh.

Mesquita, C., Dobby, H., and Mclay, A. 2016. Crab and Lobster Fisheries in Scotland: Results of Stock Assessments 2009-2012. Scottish Marine and Freshwater Science Vol 7 No 9: 73. Marine Scotland Science, Edinburgh.

Metcalfe, K., Roberts, T., Smith, R. J., and Harrop, S. R. 2013. Marine conservation science and governance in North–West Europe: Conservation planning and international law and policy. Marine Policy, 39: 289–295.

Mill, A. H., Dobby, H., and Mclay, A. 2009. Crab and lobster fisheries in Scotland: An overview and results of stock assessments, 2002-2005. Marine Scotland Science, Edinburgh.

Moland, E., and Olsen, E. 2011. Home range of European lobster (*Homarus gammarus*) in a marine reserve: implications for future reserve design. Canadian Journal of Fisheries and Aquaculture Science, 1210: 1191–1210.

Moland, E., Olsen, E. M., Knutsen, H., Garrigou, P., Espeland, S. H., Kleiven, A. R., André, C., *et al.* 2013a. Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before-after control-impact study. Proceedings of the Royal Society B, 280: 201-226.

Moland, E., Ulmestrand, M., Olsen, E. M., and Stenseth, N. C. 2013b. Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. Marine Ecology Progress Series, 491: 153–164.

Montogomery, S. 2005. Effects of trap shape, bait, and soak time on sampling the eastern rock lobster, *Jasus verreauxi*. New Zealand Journal of Marine and Freshwater Research, 39: 353–363.

Myers, R. A., Fuller, S. D., and Kehler, D. G. 2000. A fisheries management strategy robust to ignorance: rotational harvest in the presence of indirect fishing mortality. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2357–2362.

Myers, R. A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature, 423: 280–283.

Myers, R. A., and Worm, B. 2005. Extinction, survival or recovery of large predatory fishes. Philosophical Transactions of the Royal Society B, 360: 13–20. The Royal Society, London.

Pelc, R. A., Warner, R. R., Gaines, S. D., and Paris, C. B. 2010. Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences, 294: 1920–1923.

Planes, S., Jones, G. P., and Thorrold, S. R. 2009. Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences of the United States of America, 106: 5693–5697.

Prior, S. 2011. Investigating the use of voluntary marine management in the protection of UK marine biodiversity. A Report for the Wales Environment Link (WEL) Marine Working Group. Cardiff. 46 pp.

Roberts, C. 2007. The Unnatural History of the Sea: The Past and Future of Humanity and Fishing. Island Press, Washington.

Roberts, C., Hawkins, J., and Gell, F. 2005. The role of marine reserves in achieving sustainable fisheries. Philosophical transactions of the Royal Society of London B, 360: 123–32.

Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P., and Goodridge, R. 2001. Effects of Marine Reserves on Adjacent Fisheries. Science, 294: 1920–1923.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., *et al.* 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution, 20: 74–80.

Shears, N. T., Grace, R. V., Usmar, N. R., Kerr, V., and Babcock, R. C. 2006. Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. Biological Conservation, 132: 222–231.

Sheehan, E. V., Stevens, T. F., Gall, S. C., Cousens, S. L., and Attrill, M. J. 2013. Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. PLoS ONE, 8: 1–12.

Simpson, A. 1961. A Contrubtion to the bionomics of the lobster (*Homarus vulgaris*) on the coast of North Wales. Fishery Investigations, 23: 11–28.

Smith, I. P., Jensen, A. C., Collins, K. J., and Mattey, E. L. 2001. Movement of wild European lobsters *Homarus gammarus* in natural habitat. Marine Ecology Progress Series, 222: 177–186.

Smith, S. J., and Tremblay, M. J. 2003. Fishery-independent trap surveys of lobsters (*Homarus americanus*): design considerations. Fisheries Research, 62: 65–75.

Thorpe, K. E., Huntingford, F. A., and Taylor, A. C. 1994. Relative size and agonistic behaviour in the female velvet swimming crab, *Necora puber* (L.) (Brachyura, Portunidae). Behavioural Processes, 32: 235–246.

Thurstan, R. H., and Roberts, C. M. 2010. Ecological meltdown in the firth of clyde, Scotland: Two centuries of change in a coastal marine ecosystem. PLoS ONE, 5: e11767.

Tully, O., Roantree, V., and Robinson, M. 2001. Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. Journal of the Marine Biological Association of the UK, 81: 61–68.

Ungfors, A., Hallbäck, H., and Nilsson, P. G. 2007. Movement of adult edible crab (*Cancer pagurus* L.) at the Swedish West Coast by mark-recapture and acoustic tracking. Fisheries Research, 84: 345–357.

Watson, R. A., Cheung, W. W. L., Anticamara, J. A., Sumaila, U., Zeller, D., and Pauly, D. 2013. Global marine yield halved as fishing intensity redoubles. Fish and Fisheries, 14: 493–503.

Williams, P. J., Floyd, T. A., and Rossong, M. A. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). Journal of Experimental Marine Biology and Ecology, 329: 66–74.

Wood, L. 2011. Global marine protection targets: how S.M.A.R.T are they? Environmental management, 47: 525–535.

Wood, L. J., Fish, L., Laughren, J., and Pauly, D. 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx, 42: 340–351.

Wootton, E. C., Woolmer, A. P., Vogan, C. L., Pope, E. C., Hamilton, K. M., and Rowley, A. F. 2012. Increased disease calls for a cost-benefits review of marine reserves. PLoS ONE, 7: e51615.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., *et al.* 2009. Rebuilding global fisheries. Science, 325: 578–585.

Figure legends

Figure 1. Pot sampling survey locations. Baited shellfish pots were deployed in each area during July and August for four years between 2012 and 2015. The maps on the left put these sites into geographical context within the UK and the Isle of Arran. R1 represents the sampling locations within the reserve, R2 was excluded from this study, N1-N3 represent Near-control sites, and F1-F4 represent Far-control sites. Also displayed (dashed lines) are the boundaries of the Lamlash Bay fully protected marine reserve.

Figure 2. Mean catch per unit effort (cpue) of lobsters, Legal sized lobsters (>87 mm), Sublegal lobsters (<87 mm), brown crab, legal sized brown crab (>140 mm), and velvet swimming crabs within the marine reserve, Near-control and Far-control over the four year study period. Error bars represent ±1 SE.

Figure 3. Mean catch per unit effort (cpue) of Legal sized lobsters (>87 mm), Sublegal lobsters (<87 mm), brown crab, and Sublegal sized brown crab (<140 mm) plotted against distance from the boundaries of the fully protected marine reserve for all four years combined. A distance of 0 represents those sites located within the marine reserve. Error bars represent ±1 SE.

Figure 4: Mean size of brown crab, velvet crab and lobster (±1 SE) among sites located in the fully protected marine reserve, Near-control and Far-control.

Figure 5. The size structure of lobsters sampled within the fully protected marine reserve and Near- and Far-control sites across the four year study period. The number (N) of individuals sampled from each population is available in Table 2.

Figure 6. The mean estimated weight per unit effort (wpue) of lobster (±1SE) caught within the fully protected marine reserve and Near-control across the four year study period.

Figure 7. The mean weight per unit effort (wpue) of lobster and Legal sized lobster (±1SE) plotted against distance from the boundaries of the fully protected marine reserve for all four years. A distance of 0 represents those sites located within the marine reserve.

Figure 8. The mean level of damage (±1SE) exhibited in lobsters plotted against their mean size for all years and treatments combined.

Tables

Table 1. Outputs from quasipoisson GLMs used to test if treatment (reserve, near control or far control) and year (2012-2015) significantly influenced the catch per unit effort (CPUE) of lobsters, legal sized lobsters (>87 mm), sub-legal lobsters (<87 mm), brown crab, legal sized brown crab (>140 mm), sub-legal brown crab (<140 mm) and velvet swimming crabs. Significant terms are denoted with a (*).

CPUE	Deviance explained	Variable	χ2	*P*
All lobster	80.1%	Treatment	6.6	* <0.001
		Year	7.81	* <0.001
Legal lobster	71.6%	Treatment	39.1	* <0.001
		Year	3.17	* <0.001
Sub-legal lobster	88.7%	Treatment	8.2	* <0.001
		Year	5.35	* <0.001
All brown crab	80.4%	Treatment	31.11	* <0.001
		Year	18.61	* <0.001
Legal brown crab	78.7%	Treatment	4.52	* 0.006
		Year	15.31	* <0.001
Sub-legal brown crab	81.5%	Treatment	3	* 0.015
		Year	1.57	* <0.001
Velvet crab	87.3%	Treatment	41.12	* <0.001
		Year	10.25	* 0.001

Table 2. Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size distributions (% composition) of crustacean populations in the fully protected marine reserve and near and far control sites. Also displayed is the number (N) of individuals sampled from each population. Significant terms are denoted by a (*).

Species	Year	Test	N	*D*	*P*
Lobster	2012	Reserve, Near control	108; 104	0.18	0.062
	2013	Reserve, Near control	157; 104	0.27	*<0.001
	2014	Reserve, Near control	131; 98	0.48	*<0.001
	2014	Reserve, Far control	131; 545	0.58	*<0.001
	2014	Near control, Far control	98; 545	0.14	0.056
	2015	Reserve, Near control	87; 42	0.57	*<0.001
	2015	Reserve, Far control	87; 684	0.57	*<0.001
	2015	Near control, Far control	98; 684	0.42	*<0.001
Brown crab	2012	Reserve, Near control	29; 26	0.13	0.977
	2013	Reserve, Near control	14; 45	0.23	0.649
	2014	Reserve, Near control	31; 47	0.16	0.681
	2015	Reserve, Near control	70; 103	0.16	*0.002
Velvet swimming crab	2012	Reserve, Near control	230; 36	0.11	0.887
	2013	Reserve, Near control	21; 63	0.25	0.23
	2014	Reserve, Near control	94; 94	0.42	*<0.001
	2015	Reserve, Near control	114; 47	0.62	*<0.041

Table 3. Outputs from quasipoisson GLMs used to test if treatment (reserve and near control) and year (2012-2015) significantly influenced the weight per unit effort (WPUE) of lobsters, legal sized lobsters (>87 mm) and sub-legal lobsters (<87 mm). Significant terms are denoted with a (*).

WPUE	Deviance explained	Variable	χ2	*P*
All lobster	80.5%	Treatment	6836	* <0.001
		Year	1449.9	* 0.011
Legal lobster	79%	Treatment	10599	* <0.001
		Year	121.9	0.507
Sub-legal lobster	85.1%	Treatment	141.3	0.327
		Year	3107.3	* <0.001

Table 4. Outputs from a quasipoisson GLM used to test if lobster catcher unit effort (CPUE), size (mm) and treatment (reserve and near control) significantly influenced the level of damage individuals had sustained over the four year period. Significant terms are denoted with a (*).

Deviance explained	Variable	χ2	*P*
79%	Lobster CPUE	1.6	0.369
	Treatment	6.5	0.075
	Size	39.8	*<0.001

Table 5. Outputs from Pearson chi-squared tests used to compare the frequency of male and female lobsters. Significant terms are denoted by a (*).

Year	**Sex**	**Observed**	**Expected**	**χ^2**	***P***
2012	Female	73	106	20.54	*<0.001
	Male	139	106		
2013	Female	100	130.5	14.26	*<0.001
	Male	161	130.5		
2014	Female	78	114.5	23.27	*<0.001
	Male	151	114.5		
2015	Female	45	64.5	11.79	*<0.001
	Male	84	64.5		

Table 6. Outputs from Pearson chi-squared tests used to compare the frequency of male and female lobsters between the fully protected marine reserve and near control sites. Significant terms are denoted by a (*).

Year	Treatment	Test	Female	Male	χ2	*P*
2012	Near control	Observed	42	62	3.21	0.074
		Expected	35.8	68.2		
	Reserve	Observed	31	77		
		Expected	37.2	70.8		
2013	Near control	Observed	43	61	0.67	0.412
		Expected	39.8	64.2		
	Reserve	Observed	57	100		
		Expected	60.2	96.8		
2014	Near control	Observed	34	64	0.03	0.861
		Expected	33.4	64.6		
	Reserve	Observed	44	87		
		Expected	44.6	86.4		
2015	Near control	Observed	18	24	1.743	0.187
		Expected	14.7	27.3		
	Reserve	Observed	27	60		
		Expected	30.3	56.7		

Table 7. Outputs from Pearson chi-squared tests used to compare the frequency of berried and non-berried female lobsters between the fully protected marine reserve and near control sites. Significant terms are denoted by a (*).

Year	Treatment	Test	Berried	Non-berried	χ2	*P*
2012	Near control	Observed	5	37	1.48	0.224
		Expected	35.1	6.9		
	Reserve	Observed	7	24		
		Expected	5.1	25.9		
2013	Near control	Observed	4	39	1.92	0.166
		Expected	6.5	36.6		
	Reserve	Observed	11	46		
		Expected	8.5	48.4		
2014	Near control	Observed	5	29	0.06	0.811
		Expected	5.4	28.6		
	Reserve	Observed	8	40		
		Expected	7.6	40.4		
2015	Near control	Observed	1	17	3.91	*0.048
		Expected	3.6	14.4		
	Reserve	Observed	8	19		
		Expected	5.4	21.6		