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

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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

37 **Introduction**

38 The intensity and geographic reach of the world's fisheries has escalated greatly over the last two
39 centuries, causing a dramatic loss of species and fishery resources in virtually every marine ecosystem
40 on Earth (Jackson *et al.*, 2001; Myers and Worm, 2003, 2005; Roberts, 2007; Watson *et al.*, 2013;
41 Howarth *et al.*, 2014). Although many different management measures exist for maintaining and
42 supporting fish stocks, the establishment of Marine Protected Areas (MPAs) closed to some or all types
43 of fishing is considered to be one of the most effective ways to reduce mortality and boost recruitment
44 in fish stocks (Halpern and Warner, 2002; Halpern, 2003; Roberts *et al.*, 2001, 2005; Lester *et al.*, 2009).
45 In doing so, MPAs are regularly reported to increase the abundance of target species, restore size and
46 age structures, enhance reproductive output, and improve the survival and growth of juveniles (Myers
47 *et al.*, 2000; Gaines *et al.*, 2003; Grantham *et al.*, 2003; Beukers-Stewart *et al.*, 2005; Kerwath *et al.*,
48 2008; Lester *et al.*, 2009; Howarth *et al.*, 2011, 2015b). All of these effects may then result in the
49 greater production of larvae, juveniles and adults which can disperse ("spillover") outside the MPA
50 and contribute to fishery landings (McClanahan and Mangi, 2007; Harrison *et al.*, 2012).

51 If populations are to benefit from the protection afforded by MPAs, it is necessary that a number of
52 individuals spend a substantial part of their lives within their boundaries (Roberts *et al.*, 2005).
53 Lobsters, crabs and other crustaceans have therefore been proposed as ideal species for closed area
54 management thanks to their high value and relatively low mobility (Follesa *et al.*, 2009, 2011; Moland
55 and Olsen, 2011; Moland *et al.*, 2013b). In fact, several studies have found the abundance of lobsters
56 to increase within MPAs 2-25 fold (Shears *et al.*, 2006; Fenberg *et al.*, 2012; Moland *et al.*, 2013a) and
57 that such increases can become evident after just 18 months of protection (Hoskin *et al.*, 2011).
58 Studies also report increases in mean body size (Hoskin *et al.*, 2011; Moland *et al.*, 2013a) and
59 increased catches in neighbouring fishing grounds (Goñi *et al.*, 2006, 2010; Díaz *et al.*, 2011). Then
60 again, other studies suggest MPAs can displace fishing effort to surrounding areas (Bohnsack, 2000;
61 Dinmore *et al.*, 2003; Kaiser, 2005) and that the greater densities of target species within MPAs may

62 lead to greater levels of disease transmission, aggression and physical injury (Wootton *et al.*, 2012;
63 Davies *et al.*, 2014). Also, as MPAs do not address the factors underlying overfishing, many argue that
64 MPAs should be complemented with restrictions on fishing effort and fishing gears, all of which have
65 received mutual consent from fishers and managers (Hilborn, 2007; Worm *et al.*, 2009; Khan and Neis,
66 2010).

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

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

84 **Methods**

85 **Scottish crustacean fisheries**

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

102 **Sampling design**

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

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

120 Targeted surveys were conducted during one week in mid-July and one week in mid-August for four
121 years between 2012 and 2015. The catchability of crustaceans varies considerably depending on moult
122 stage, reproductive condition, size, sex, seasons, habitats, water temperature and the number of
123 crustaceans already in a trap (Smith and Tremblay, 2003; Jury *et al.*, 2007). Hence, averaging catch
124 rates over the two months was intended to account for any shorter-term fluctuations in catchability.
125 Crustaceans were sampled using standard specification commercial shellfish pots of two-side eye
126 entrance design. Mesh size was 65 mm and pots measured 64 x 38 x 41 cm, with two entrances
127 measuring 21 x 18 cm. Pots were baited with a mix of mackerel (*Scomber scombrus*) and redfish
128 (*Sebastes* spp) and deployed in fleets of five with 20 m between each pot. Marker-buoys were
129 attached to both ends of the fleets, and pots were considered heavy enough to act as their own
130 anchor. For each day of sampling, three fleets were deployed within and outside the reserve parallel
131 to the shore. These were then left to "soak" for approximately 48 hours before being hauled. In 2012,
132 a total of 32 fleets were deployed over the two sampling periods (i.e. 16 in July and 16 in August), half
133 of which were within the reserve and the other within the near control. In 2014 and 2015, this number
134 increased to 36 fleets. However, in 2013, one fleet of pots intended for outside the reserve in July was
135 inadvertently deployed inside. Hence, during this year, 19 sites were sampled within the reserve and
136 17 outside.

137 For the years subsequent to 2012, targeted surveys were bolstered with additional fishing
138 observations made aboard two different commercial potting vessels. These took place between July-
139 August within the far control sites (F1-F4) 10-20 km south of the marine reserve. The methods used
140 during these observations differed slightly from the targeted surveys in that fleets varied between 5-
141 10 pots in length and were left to soak between 48-72 hours. While these differences have the
142 potential to inflate catches, it has been observed that when soak times are five days or less, small
143 variations in soak time have no significant effect on the catch rate of lobster (Bennet and Edwards,
144 1981a; Montgomery, 2005). In addition, our measurements of Catch Per Unit Effort (CPUE) were
145 based upon the average number of individuals caught per pot, negating the impact of varying fleet
146 lengths.

147 **Data collection**

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

159 **Tagging**

160 All lobsters (2012-2015) and brown crabs (2012 only) caught in this study were marked with a double
161 T-bar anchor tag (Hallprint Pty. Ltd) measuring 55mm in length. These tags were selected for their

162 quick application and high rate of retention during moulting (González-Vicente *et al.*, 2012). Each tag
163 was imprinted with a unique identification number, a telephone number, and coloured either green
164 or orange depending on whether individuals were caught from within or outside the reserve
165 respectively. Tags were inserted using a Monarch Marking 3030 tagging gun. Lobsters were tagged in
166 their abdominal muscle immediately behind the posterior edge of the carapace, either side of the
167 midline, to avoid puncturing the dorsal abdominal artery and the gut (Smith *et al.*, 2001). Brown crabs
168 were tagged where their fourth leg (on either side) joined the rear of the carapace. Geographical
169 coordinates of capture were recorded every time a tagged individual was recaptured either by our
170 potting surveys, or by local fishermen cooperating with this study. Velvet swimming crabs were not
171 tagged due to their small size relative to the tags we had available.

172 **Data analyses – comparisons of CPUE**

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

$$178 \quad \text{CPUE} = \frac{\text{Number of individuals caught in fleet}}{\text{Number of pots in fleet}}$$

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

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

197 **Comparisons of size and weight**

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

$$203 \text{ Weight of male lobster (g)} = 0.0022 \times \text{length}^{2.7416}$$

$$204 \text{ Weight of female lobster (g)} = 0.0016 \times \text{length}^{2.8134}$$

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

$$207 \text{ WPUE (g)} = \frac{\text{Total weight of lobster in fleet}}{\text{Number of pots in fleet}}$$

208 As with CPUE, the WPUE of lobsters was compared among treatments and years using quasipoisson
209 GLMs. The mean WPUE of lobsters was also calculated for all sites within the reserve, as well as 0.5
210 km, 1 km, and 1.5 km away. These data were then plotted against distance. Trends between distance

211 and WPUE were tested for significance by calculating Spearman's rank correlation coefficient.
212 Distances greater than 1.5 km could not be used as these data were collected from the far control
213 where data on undersized individuals had been recorded inconsistently.

214 **Comparisons of gender ratios and fecundity**

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

$$222 \quad \text{Potential reproductive output} = (1.554 \times \text{length}) - 10286$$
$$223 \quad \text{(number of eggs per female)}$$

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

227 **Comparisons of damage**

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

235
$$\text{Damage (\%)} = \frac{\text{Damage (score)}}{36} \times 100$$

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

238

239 **Results**

240 **Catch rates**

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

258 (± 0.03 SE) over the four year study period. However, this variation in temperature had not significantly
259 influenced catch rates of lobster (GAM; Deviance = 3.1%; $\chi^2 = 263.2$; $P > 0.05$).

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

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

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

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

287 **Lobster movements and growth**

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

295 **Size and weight distributions**

296 The mean size of lobsters was 10 and 15 mm greater (ANOVA, $F_{(2,869)} = 23.8$, $P < 0.001$) within the
297 reserve compared to near and far control sites respectively (Figure 4). Likewise, velvet swimming crabs
298 were 2mm larger within the reserve than both controls (ANOVA, $F_{(1,159)} = 4.2$, $P < 0.05$). In contrast,
299 brown crabs were 25 mm larger within the near control compared to the marine reserve (ANOVA,
300 $F_{(1,171)} = 14.3$, $P < 0.05$).

301 Comparing the overall size distribution of crustaceans also revealed differences among treatments.
302 Lobster populations within the marine reserve were composed of larger individuals for all years of
303 study (Table 2). In fact, large lobsters >111 mm were entirely absent in the near and far controls (Figure
304 5). Likewise, large velvet swimming crabs >80 mm were absent in the near control. However,
305 significant differences among treatments only occurred in 2014 and 2015 when sample sizes of velvet

306 crabs were much higher. During these two years, velvet crabs displayed a peak size of 71-75 mm within
307 the reserve compared to 61-65 mm in the near control. Similarly, brown crabs only exhibited a
308 significant difference among treatments in 2015, when sample sizes for this species were also much
309 greater. In this year, the size of brown crabs peaked at 91-100 mm within the reserve but peaked
310 substantially higher at 161-170 mm within the near control.

311 Differences in the weight of lobster caught per pot were also observed between treatments (Figure
312 6). These were initially minor during the first year of study but by 2015 the average fleet of 5 pots set
313 inside the reserve yielded 3.5 kg of lobster (SE \pm 0.03) compared to just 1.5 kg (SE \pm 0.05) outside the
314 reserve; a significant difference of 133% (Table 3). Similar to CPUE, these differences in WPUE were
315 more pronounced for lobsters of legal landing size which were 233% higher within the reserve
316 compared to outside. Again, as was observed with CPUE, the WPUE of lobster increased 26% within
317 the reserve and decreased 11% outside between 2012 and 2013, before experiencing a 27% decline
318 for the final two years of study across all treatments. Like before, the WPUE of all lobsters (Spearman's
319 rank; $N = 140$; $R = -0.42$; $P < 0.001$) and legal sized lobsters (Spearman's rank; $N = 140$; $R = -0.45$; $P <$
320 0.001) significantly declined with increasing distance from the boundaries of the fully protected
321 marine reserve (Figure 7) as pots set within the reserve yielded 100% more lobster biomass compared
322 to pots set 1, 1.5 and 2 km away.

323 **Damage and disease**

324 Statistical analyses of shell disease and damage levels were difficult due to very low occurrences of
325 both. In terms of disease, only 18 lobsters (out of 2449 = 0.73%) and 20 brown crabs (out of 1113 =
326 1.8%) displayed any sign of disease across the entire study period. Similarly, only 36 brown crabs
327 (3.23%) showed signs of damage. However, 114 lobsters (4.6%) were damaged which allowed for
328 statistical analysis. Damage in lobsters ranged from 0% (no damage) to 44.4% (individual missing 1
329 claw and 6 legs). Mean damage scores for lobsters located within the marine reserve were 1.9 times
330 higher than for those located outside. The combination of higher lobster catches (potentially

331 correlated with competition) and levels of damage within the reserve, suggested that greater lobster
332 CPUE resulted in more damage. However, a GLM revealed that the level of damage an individual had
333 sustained was solely related to its size (Table 4). In fact, large lobsters > 110 mm had sustained over
334 218% more damage than smaller individuals irrespective of whether they were sampled from within
335 or outside the reserve (Figure 8).

336 **Lobster gender ratios and fecundity**

337 Catches of male lobster were higher than females in all treatments across all years (Table 5). However,
338 comparisons among treatments revealed that there was no difference in the frequency of male and
339 female lobsters between the reserve and near control (Table 6). More than twice as many berried
340 lobsters were caught within the reserve than the near control for every year of study, yet 2015 was
341 the only year where this difference was significant (Table 7). Nonetheless, the mean potential
342 reproductive output per female lobster was 22.1% greater within the reserve than outside (Mann-
343 Whitney: $U = 8075$, $N = 296$, $P < 0.001$). Overall, the total reproductive output (i.e. the sum of the
344 reproductive potential of each female lobster) was 70% greater than the near control, equivalent to
345 46,000 more eggs within the areas sampled.

346

347 **Discussion**

348 This study provides evidence that, after nearly seven years of protection, the fully protected marine
349 reserve in Lamlash Bay is benefitting commercially important populations of European lobster by
350 increasing their catches, body size and reproductive output. Furthermore, as lobsters are migrating
351 from within the reserve to outside, these benefits are likely being transferred to neighbouring fishing
352 grounds. Then again, the greater densities of large adult lobsters (inferred from higher catch rates)
353 appear to be predated and / or competitively displacing juvenile lobsters, brown crabs and velvet
354 swimming crabs from the area. Combined with our previous work at this location (see Howarth *et al.*,
355 2011, 2015a, 2015b), this study provides further evidence that temperate marine reserves can deliver

356 fisheries and conservation benefits, but that recovery is not straight forward, as the recovery of some
357 species can have knock-on effects on others.

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

371 Catch rates of berried lobster were twice as high within the reserve as outside. If there was a greater
372 proportion of females within the reserve this trend would have been easily explained, as more females
373 should equate to more berried females. However, as we observed no difference in sex ratios between
374 the reserve and outside, it is more likely a consequence of lobsters being larger within the closed area.
375 To explain, female lobsters reach sexual maturity at approximately 77 mm in size, or 4-12 years old in
376 age (Simpson, 1961; Barreto and Bailey, 2015). As catch rates of large-bodied adults were lower
377 outside the reserve it is likely that sexually mature, berried female lobsters were less abundant. Added
378 to this, berried female lobsters exhibit less mobility and therefore lower catchability than non-berried
379 females (Agnalt *et al.*, 2007) further lowering the probability of catching berried lobsters outside the
380 reserve. Interestingly, this study caught significantly more males than females. However, government

381 reports indicate male and female lobsters are generally landed in equal proportions in Scotland (Mill
382 *et al.*, 2009). Again, this could be explained by the lower catchability of berried lobsters which would
383 reduce the number of females caught both within and outside the reserve. Whichever the reason, it
384 has been legal to land berried lobsters in the UK since 1966 (Bennet and Edwards, 1981b), meaning
385 the marine reserve should act as a safe haven for sexually mature lobsters, allowing them to
386 contribute to recruitment.

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

396 Although lobster catches have increased within the reserve compared to surrounding areas, they have
397 not followed a clear upward trajectory. When our surveys began in 2012, there was almost no
398 difference in CPUE between the reserve and near control. However, lobster catches increased within
399 the reserve during the following year. Lobster catch rates either then stabilised or declined across all
400 treatments for the final two years of study. Importantly, the marine reserve appears to have buffered
401 wider declines as positive differences between the reserve and surrounding fishing grounds were
402 maintained, and in some cases increased, during this period. But the question remains, why did lobster
403 CPUE decrease between 2014 and 2015, and why would these declines affect those lobsters within
404 the marine reserve? An obvious explanation would be that lobster stocks within the Firth of Clyde are
405 under intensive fishing pressure. Between 2009 and 2012 (the latest available assessment) both males

406 and females were reported as being fished above Maximum Sustainable Yield (MSY; Mesquita *et al.*,
407 2016). There have also been reports of increased fishing activity along the boundaries of the reserve
408 over the last four years (Andrew Binnie, COAST, personal observation). Added to this, catches of
409 undersized lobsters declined between 2012 and 2015, suggesting very little recruitment had occurred
410 during this period. Together, this evidence suggests that increasingly high numbers of lobster were
411 being removed through fishing and not being replaced by recruitment. As lobsters from within the
412 reserve were spilling over to neighbouring fishing grounds, they too were capable of being taken by
413 the fishery. This may explain why CPUE declined both within and outside the reserve.

414 Despite our positive results, the 109% difference in lobster CPUE between Lamlash Bay marine reserve
415 and surrounding areas is less than those documented by other MPA studies. In the Lundy MPA, which
416 is only slightly larger than the one in Lamlash Bay, the CPUE of European lobsters was 171% higher
417 within the reserve than control sites after just four years of protection (Hoskin *et al.*, 2011). Likewise,
418 several MPAs off the coast of Norway, all similar in size to Lamlash Bay, increased lobster CPUE by
419 245%, again after just four years of protection (Moland *et al.*, 2013a). Along with the factors discussed
420 above, it is likely that limited amounts of suitable lobster habitat in the Lamlash reserve may be
421 responsible for the smaller differences in our study. Previous surveys in the area (Howarth *et al.*, 2011,
422 2015a, 2015b) revealed that the rocky and boulder habitats preferred by lobsters (Mehrtens *et al.*,
423 2005; Mill *et al.*, 2009; Barreto and Bailey, 2015) are only present along the southern edge of the
424 reserve. This could be reducing the amount of area within the reserve available for lobster habitation,
425 which would limit the extent of any benefits the fully protected marine reserve can bestow on
426 lobsters. This highlights that marine reserves must be well designed to maximise their effectiveness;
427 incorporating suitable habitat and being of adequate size to protect species of interest (see Edgar *et*
428 *al.*, 2014). For brown crabs, their high mobility and extensive seasonal migrations to offshore spawning
429 grounds (Bennett and Brown, 1983) is likely to constrain any benefits they may receive from
430 protection. Consequently, the small size of Lamlash Bay marine reserve may, at best, only provide
431 protection during a very limited part of their annual range. Much larger protected areas encompassing

432 aggregation sites or spawning areas would probably be necessary if closed areas were to be of any
433 benefit to this species (Ungfors *et al.*, 2007). In contrast to brown crabs, the movements of velvet
434 crabs are thought to be restricted to a few hundred metres (Baretto and Bailey, 2015). Although this
435 makes them an ideal candidate for protection, stocks are only seasonally/ lightly exploited, meaning
436 their response to protection will also likely be limited.

437 Higher densities of target organisms can lead to greater levels of disease transmission and physical
438 injury (Davies *et al.*, 2014; Howarth *et al.*, 2014). For example, both Wooton *et al.*, (2012) and Davies
439 *et al.*, (2014) found higher damage rates in large lobsters in Lundy MPA, and highlighted this as a
440 potentially negative effect of marine reserves. This is because lobsters are solitary, territorial animals
441 and are well known to fight each other when in close proximity (Debusse *et al.*, 1999; Williams *et al.*,
442 2006). Given the higher abundance of lobsters within Lamlash bay, we too expected lobsters within
443 the closed area to show higher levels of damage. Consistent with this, lobsters located within the
444 Lamlash Bay marine reserve were 1.9 times more damaged than those outside However, unlike what
445 was observed in Lundy, a GLM revealed that the level of damage an individual had sustained was solely
446 related to its body size, and not CPUE as expected. In fact, large lobsters greater than 110 mm had
447 sustained over 218% more damage compared to smaller individuals, regardless of whether they were
448 captured within or outside the reserve. This trend may be explained by four combining factors: (1)
449 large lobsters are usually stronger, have a greater ability to inflict injury, and are therefore more likely
450 to win a fight (Karnofsky *et al.*, 1989; Thorpe *et al.*, 1994; Huber and Kravitz, 1995; Huber *et al.*, 1997;
451 Arnott and Elwood, 2009); (2) lobsters that win a fight are more likely to win a subsequent one, and
452 are therefore less likely to stand down from a fight (Huber *et al.*, 1997); (3) larger individuals would
453 be older, and therefore would have had more opportunities to become subject to attack and injury
454 than smaller individuals; and (4) larger lobsters moult less frequently than smaller ones, hence
455 accumulated damage may be slower to repair in large individuals (Hughes and Matthiesen, 1962).
456 Overall though, we observed much lower levels of damage compared to the MPA in Lundy (4.65 %
457 compared to 33 %) and almost no disease (0.73% compared to 24%; Davies *et al.*, 2014).

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

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

483 suggesting that competition / predation between velvet crabs and lobster may be weaker than for
484 brown crabs.

485 Following a large number of recently established policies and initiatives, the global coverage of MPAs
486 is set to increase dramatically over the next decade (Wood *et al.*, 2008; CBD, 2011; Harrop, 2011;
487 Wood, 2011; Fenberg *et al.*, 2012; Jones, 2012; Metcalfe *et al.*, 2013; JNCC, 2016;). However, studies
488 into the effects of MPAs remain relatively scarce in temperate and cold waters, and are particularly
489 limited in Europe and the UK (Fenberg *et al.*, 2012). Out of the few that do exist, the majority have
490 investigated changes in specific ecological or fishery components, rather than investigating the
491 ecosystem as a whole, either focusing solely on benthic habitats (e.g. Sheehan *et al.*, 2013) or just one
492 or two species of commercial importance (Beukers-Stewart *et al.*, 2005; Hoskin *et al.*, 2011; Moland
493 *et al.*, 2013a). However, our research within Lamlash Bay (this study and Howarth *et al.*, 2011, 2015a,
494 2015b) has shown that a wide range of species and habitats can benefit from protection, but far from
495 all. Hence, our work highlights that it is far more valuable to study as many components of the
496 ecosystem as possible, rather than one alone. This study also highlights marine reserves must be well
497 designed if they are to be of benefit to the species they intend to protect. The small size of Lamlash
498 Bay marine reserve offers little benefit to brown crabs, and the lack of suitable habitat probably caps
499 benefits to lobsters. For reasons such as these, it is unlikely that small MPAs alone (such as Lamlash
500 Bay) will be enough to counter the high levels of fishing mortality and low levels of recruitment
501 currently being reported in several major crab and lobster stocks around Scotland (Tully *et al.*, 2001;
502 Mill *et al.*, 2009; Barreto and Bailey, 2013, 2015; Mesquita *et al.*, 2016;). At present, shellfish fisheries
503 within the Firth of Clyde are only managed through minimum legal landing size. However, it is widely
504 agreed that a combination of managing fishing effort, fishing gears and establishing protected areas,
505 all of which have received mutual consent from managers, fishermen and other stakeholders, is by far
506 the most effective way to restore stocks and marine ecosystems (Hilborn, 2007; Worm *et al.*, 2009;
507 Khan and Neis, 2010;).

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517

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749 **Figure legends**

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

757 **Figure 2.** Mean catch per unit effort (cpue) of lobsters, Legal sized lobsters (>87 mm), Sublegal lobsters
758 (<87 mm), brown crab, legal sized brown crab (>140 mm), and velvet swimming crabs within the
759 marine reserve, Near-control and Far-control over the four year study period. Error bars represent ± 1
760 SE.

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

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

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

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

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

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

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790 **Tables**

791

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

CPUE	Deviance explained	Variable	χ^2	<i>P</i>
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

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797 **Table 2.** Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size
 798 distributions (% composition) of crustacean populations in the fully protected marine reserve and near
 799 and far control sites. Also displayed is the number (N) of individuals sampled from each population.
 800 Significant terms are denoted by a (*).
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Species	Year	Test	N	<i>D</i>	<i>P</i>
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

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

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WPUE	Deviance explained	Variable	χ^2	<i>P</i>
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

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

Deviance explained	Variable	χ^2	<i>P</i>
79%	Lobster CPUE	1.6	0.369
	Treatment	6.5	0.075
	Size	39.8	* <0.001

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

Year	Sex	Observed	Expected	χ^2	<i>P</i>
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		

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

Year	Treatment	Test	Female	Male	χ^2	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		

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

Year	Treatment	Test	Berried	Non-berried	χ^2	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		

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