# Effects of marine reserves in the context of spatial and temporal variation: an analysis using Bayesian zero-inflated mixed models

**Adam N. H. Smith[1],\*, Marti J. Anderson[2], Russell B. Millar[3], Trevor J. Willis[4]**

[1]Institute for Natural and Mathematical Sciences, Massey University Albany, Private Bag 102904, Auckland 0745, New Zealand

[2]New Zealand Institute for Advanced Study, Massey University Albany, Private Bag 102904, Auckland 0745, New Zealand

[3]Department of Statistics, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

[4]Institute of Marine Sciences, School of Biological Sciences, University of Portsmouth, Ferry Road, Eastney, Portsmouth P04 9LY, United Kingdom

ABSTRACT: Evaluating the effects of marine reserves on exploited species can be challenging because they occur within a context of natural spatial and temporal variation at many scales. For rigorous inferences to be made, such evaluations require monitoring programs that are replicated at appropriate scales. We analysed monitoring data of snapper *Pagrus auratus* (Sparidae) in north-eastern New Zealand, comprised of counts from baited-underwater-video surveys from inside and outside three marine reserves, replicated at many levels. Surveys included areas inside and outside of marine reserves, at each of three locations, in each of two seasons, over a period of up to 14 years, in an unbalanced design. The Bayesian modelling approach allowed the use of some familiar aspects of analysis of variance (ANOVA), including mixed models of fixed and

\*Email: anhsmith@gmail.com

24  random effects, hierarchically nested structures, and variance decomposition, while allowing for

25  overdispersion and excess zeros in the counts. Model selection and estimates of variance

26  components revealed that protection by marine reserves was by far the strongest measured source

27  of variation for relative densities of legal-sized snapper. The size of the effect varied across years

28  among the three reserves, with relative densities being between 7 and 20 times greater in reserves

29  than in nearby areas. Other than the reserve effect, the temporal factors of season and year were

30  generally more important than the spatial factors at explaining variation in counts. In particular,

31  overall relative densities were ~ 2–3 times greater in autumn than in spring for legal-sized

32  snapper, though the seasonal effect was also variable among locations and years. We consider

33  that the Bayesian generalised linear mixed modelling approach, as used here, provides an

34  extremely useful and flexible tool for estimating the effects of management actions and

35  comparing them directly with other sources of spatial and temporal variation in natural systems.

36

37  KEY WORDS: Baited underwater video (BUV) · Bayesian analysis · generalised linear mixed

38  models · marine reserves · snapper *Pagrus auratus* · overdispersion · variance components · zero

39  inflation

40

41                                    **INTRODUCTION**

42          The exploitation of marine species by humans has caused the depletion of many stocks of

43  fishes worldwide (Pauly et al. 2005, Worm & Branch 2012). No-take marine reserves, designated

44  areas in which all harvesting and damaging of marine life is prohibited (Lubchenco et al. 2003),

45  are increasingly being used as part of the effort to ameliorate this trend. If sufficiently enforced,

46  marine reserves have been shown to increase the size and abundance of exploited species within

47  their borders (Mosqueira et al. 2000, Micheli et al. 2004, Claudet et al. 2010, Babcock et al.

48    2010). This may, in turn, produce secondary ecological effects, such as enhancing populations of

49    exploited species beyond the boundaries of the reserve (Roberts & Polunin 1991, Dugan & Davis

50    1993, Stoner & Ray 1996, Bohnsack 1998) or facilitating changes in habitat through trophic

51    cascades (Babcock et al. 1999, Shears et al. 2008, Leleu et al. 2012). The value of marine

52    reserves is primarily as a means to manage and protect exploited or endangered species in a

53    particular area, which may then produce broader benefits in terms of increased biodiversity and

54    ecosystem function.

55        For marine reserves to be used effectively as a management tool, it is critical to be able to

56    estimate and predict their effects. Studies that monitor the abundance of exploited species in

57    existing marine reserves are an essential source of information on which to base such predictions.

58    Accurately quantifying the effects of marine reserves on exploited species can be challenging,

59    however. Data from such studies, often in the form of counts, can be overdispersed or contain

60    excess zeros (Smith et al. 2012), requiring statistical models to be based on nonstandard

61    distributions. Furthermore, marine ecosystems exhibit considerable variation at several temporal

62    and spatial scales (Underwood et al. 2000). Hierarchical sampling regimes that span these scales

63    of variation are therefore necessary in order to obtain rigorous estimates of the effects of reserves

64    (Andrew & Mapstone 1987, García-Charton & Ruzafa 1999, García-Charton et al. 2000, Willis et

65    al. 2003b). For example, if the abundance of an organism varies from year to year, then a study

66    that spans a number of years will enable far more accurate estimates of long-term effects, as well

67    as providing information on inter-annual variation. The extent to which abundance varies in time

68    and space at different scales is interesting in itself, and provides a context of the underlying,

69    'natural' variation with which to compare any measured effect of marine reserves. While some

70    authors have stressed the need to make such comparisons (García-Charton & Ruzafa 1999,

71 García-Charton et al. 2000, 2004), appropriate statistical methods for directly comparing sources

72 of variation in studies of reserve effects have not been explicitly specified.

73       Here, we analyse a long-term, spatially replicated monitoring dataset of counts of snapper

74 *Pagrus auratus* (Sparidae) from areas inside and outside each of three marine reserves in north-

75 eastern New Zealand. The analysis used a Bayesian approach outlined by Gelman (2005) for

76 analysis of variance (ANOVA), which was extended here to more complex zero-inflated

77 generalised linear mixed models (GLMMs). This approach easily incorporated the unbalanced

78 hierarchical structure of the study design in combination with nonstandard error distributions to

79 allow for overdispersion and excess zeros. The primary aim was to estimate the effects of marine

80 reserve protection on counts of snapper, while simultaneously accounting for other sources of

81 variation at various spatial and temporal scales. We then compared the estimated reserve effects

82 with other sources of variation in the study design using variance components. The consistency of

83 reserve effects in time and space was also evaluated by estimating interactions between the

84 reserve effect and other factors.

85

86       **MATERIALS AND METHODS**

87       **Background and sampling design**

88       Snapper is an important coastal species in temperate north-eastern New Zealand,

89 supporting the country's largest inshore commercial and recreational fisheries (Maunder & Starr

90 2001). Stocks of snapper in this region (SNA1) are believed to be slowly rebuilding since being

91 heavily exploited and reduced below the maximum sustainable yield in the latter half of the 20th

92 century (Ministry for Primary Industries 2013). Snapper is also ecologically important, with

93 strong evidence that its predation of sea urchins (*Evechinus chloroticus*) can contribute to a

94 trophic cascade that allows the restoration of kelp (*Ecklonia radiata*) forests within marine

95    reserves in some contexts (Babcock et al. 1999, Shears et al. 2008). There is also some evidence

96    that small crypto-benthic fishes may be affected by large densities of snapper in a marine reserve

97    (Willis & Anderson 2003).

98          An ongoing monitoring program of the relative density of snapper in areas inside and

99    outside (adjacent to) marine reserves at three locations in the north-eastern bioregion of New

100   Zealand, namely Leigh, Tawharanui, and Hahei (Table 1, Fig. 1), began in 1997. These three

101   locations have broadly similar habitat and environmental conditions (Shears et al. 2008). Refer to

102   Willis et al. (2003a) for a description and analysis of the first three years of data and Drake

103   (2006) for preliminary Bayesian modelling of the data from Leigh only. The program used a

104   baited-underwater-video (BUV) sampling method (Willis & Babcock 2000), which was

105   developed following reports that snapper were differentially attracted to divers within reserves

106   compared to outside reserves, thereby introducing bias into the usual method of underwater

107   visual surveys (Cole 1994). The data are in the form of counts, taken as the maximum number of

108   snapper seen in any one frame of a 30 min-long underwater video deployment ("MaxN"). This is

109   assumed here to be a measure of the relative density of snapper. Snapper were divided into those

110   below ("sublegal") and above ("legal") the recreational minimum legal size of 27 cm fork length

111   (scheduled to increase to 30 cm in April 2014), and these two size classes were modelled

112   separately.

113          At each of the three locations, the coastline was divided into a number of areas, some

114   falling inside and some falling outside the marine reserves (Fig. 1). Note that at each location, the

115   areas falling outside of the reserve occurred in both directions along the coastline, to avoid spatial

116   confounding of areas with reserve effects. Monitoring surveys began in 1997 and occurred twice

117   per year in each of two seasons: spring (primarily September–December) and autumn (primarily

118   March–June), but surveys were not repeated consistently at all locations after the autumn survey

119    of 1999, yielding an overall sampling design that is highly unbalanced in its cell structure (Table

120    2). The two seasons were included in the monitoring design because some individuals of this

121    species undergo a seasonal inshore migration which causes inshore densities to increase during

122    summer months and subsequently decline during winter months (Willis et al. 2003a, Willis &

123    Millar 2005). At the time of each survey done at a particular location, $n = 3–6$ (usually 4)

124    replicate BUV deployments were done at haphazardly chosen positions within each area. A total

125    of $n = 1045$ deployments were included in the models described here (Table 2). This sampling

126    design yielded five factors: Reserve (fixed with 2 levels, inside and outside), Season (fixed with 2

127    levels, autumn and spring), Year (random with up to 12 levels), Location (fixed with 3 levels)

128    and Areas (random, nested in Reserve $\times$ Location, with up to 6 levels per combination of reserve-

129    by-location, see Fig. 1). We chose to treat Location as a fixed effect because the focus was to

130    estimate the effects for these particular reserves, rather than for reserves in general. Furthermore,

131    with only three locations, there was little information with which to estimate a variance

132    parameter.

133

134                           **Candidate models and model selection**

135             Counts of sublegal and legal snapper from the monitoring program were analysed using

136    Bayesian zero-inflated generalised linear mixed models (GLMMs). Following Gelman (2005),

137    we used the Bayesian approach to model variation associated with the effects of marine reserves,

138    as well as seasons, locations, areas, and years, in a structured analysis-of-variance (ANOVA)

139    framework. The term ANOVA is used here to refer specifically to the structuring of the

140    coefficients into 'batches', so that the levels of each categorical factor are grouped together.

141    Variance components are estimated for each batch of coefficients in order to compare the relative

142    importance of the terms in the model. In our models, Gelman's (2005) framework was extended

143    to include error structures considerably more complex than that of traditional Gaussian ANOVA,

144    as required to account for overdispersion and zero inflation.

145        Models were implemented using Markov chain Monte Carlo (MCMC) methodology with

146    the software OpenBUGS (Lunn et al. 2009), called from within R (R Development Core Team

147    2013) by the R2OpenBUGS library (Sturtz et al. 2005). Each model was run with three chains,

148    each having a length of 100,000 iterations, from which a burn-in of 50,000 was discarded. The

149    chains were thinned at a rate of 1 in 5, resulting in a total of 30,000 values being kept for each

150    model. Convergence was checked using the Brooks-Gelman-Rubin statistic (Gelman & Rubin

151    1992, Brooks & Gelman 1998).

152        The full five-factor experimental design, including all of the potential interactions among

153    factors, was highly complex, having a total of 19 terms (Table 3). Due to the number of missing

154    cells in the sampling design (Table 2) leading to non-identifiability, heuristics were used first to

155    identify appropriate candidate predictor terms for model selection. Specifically, candidate terms

156    for model selection did not include interactions higher than third order and also did not include

157    the third-order interaction that did not involve Reserves (i.e. Season $\times$ Year $\times$ Location, see Table

158    2). A formal model-selection procedure was then used to choose the most favourable model out

159    of hundreds of remaining available candidate models for each of the sublegal- and legal-sized

160    snapper datasets.

161        The candidate models differed in two key respects: the structure of the distribution of

162    errors, and the factors (including interactions) that were included. The base distributions

163    considered for the errors were zero-inflated Poisson (ZIP) and the zero-inflated negative binomial

164    (ZINB). The ZIP and ZINB both had as parameters $\lambda$, the mean of the Poisson distribution

165    conditional on the absence of excess zero, and $\pi$, the probability of the occurrence of an excess

166   zero. In addition, the ZINB had the parameter $\delta$ which allowed for aggregation (overdispersion)

167   in the counts. For either of these error distributions, the overall mean is given by

168                                $\mu = (1-\pi)\lambda.$                                (1)

169          The conditional mean, $\lambda$, was modelled as a linear predictor of candidate terms with a log-

170   link function. Zero inflation, $\pi$, was incorporated using one of four alternative types of models

171   (Smith et al. 2012): (1) no zero inflation ($\pi = 0$); (2) constant zero inflation ($\pi = \alpha$, where $\alpha$ is a

172   single constant parameter to be estimated); (3) zero inflation is linked to the conditional mean

173   (Liu & Chan 2011, Smith et al. 2012); and (4) zero inflation modelled as a separate linear

174   predictor of the candidate terms with a logit-link function. A computing cluster with multiple

175   processors allowed us to conduct a thorough search for the best combination of terms (including

176   two- and three-way interactions; see Table 3) for modelling $\lambda$, and also $\pi$ in the case of zero

177   inflation by way of a separate model (type 4 above). The general approach began by fitting the

178   most complex model with the full set of candidate terms (as listed in Table 3). A batch of models

179   was then run, where each model had one of the poorest performing terms removed, and then the

180   process was repeated. Third-order interactions were removed prior to second-order interactions,

181   in a logical sequence, and no models included interaction terms involving the main effects that

182   were not also included in the candidate model. This approach for selecting appropriate terms was

183   done separately for both types of error distribution, and for all four types of zero-inflated model

184   for estimating $\pi$.

185          Model selection was based on the Deviance Information Criterion (DIC, Spiegelhalter et

186   al. 2002, Millar 2009), using half the variance of the posterior deviance for estimating the

187   effective number of parameters $p_D$ (Gelman et al. 2004). Some models were excluded because of

188   very high variance in the posterior distributions of some parameters, which was probably caused

189 by poor identifiability (Omlin & Reichert 1999). The final models were chosen, from those that

190 remained, to be those with the fewest parameters within two units of the lowest DIC score.

191

192 **Structure of the selected models**

193 For both sublegal- and legal-sized snapper, the count ($y$) in replicate $m$ in year $l$, area $k$

194 (nested in Reserve $\times$ Location), Location $j$, Season $i$, and Reserve status $h$, was best modelled

195 using the negative binomial distribution as follows:

$$y_{hijklm} \sim \mathrm{ZINB}(\lambda_{hijkl}, \pi_{hijkl}, \delta). \tag{2}$$

197 For sublegal-sized snapper, the linear predictor for the conditional mean was:

$$\log(\lambda_{hijkl}) = \beta_0 + S_i + L_j + A_{k(j)} + Y_l + (SL)_{ij} + (SY)_{il} + (LY)_{jl} \tag{3}$$

199 and excess zeros required the use of a separate linear predictor (type 4), namely

$$\log\left(\frac{\pi_{hijkl}}{1-\pi_{hijkl}}\right) = \beta_0^{(\pi)} + L_j^{(\pi)} + A_{k(j)}^{(\pi)}. \tag{4}$$

201 For legal-sized snapper, the linear predictor for $\lambda$ was

$$\log(\lambda_{hijkl}) = \beta_0 + R_h + S_i + L_j + A_{k(h \times j)} + Y_l + (RL)_{hj} + (RY)_{hl} + (SL)_{ij} + (SY)_{il} \tag{5}$$

203 and the model for the zero inflation parameter was

$$\log\left(\frac{\pi_{hijkl}}{1-\pi_{hijkl}}\right) = \gamma_0 + \gamma_1 \log(\lambda_{hijkl}) \tag{6}$$

205 using Smith et al.'s (2012) "linked" model where estimates of both the mean conditional count

206 and the rate of excess zeros are based on a single set of estimated coefficients (type 3). In

207 equations (3)–(5), $\beta_0$ is an overall fitted mean and the subsequent abbreviations correspond to

208 parameters for individual terms in the model as indicated in Table 3. Within each factor, the

209 coefficients were centred on zero (see equation 9 below), so that estimates of mean counts of

210 interest (e.g. the overall mean within reserves) could be constructed based on the above

211 equations, where the values of $\lambda$ and $\pi$ are obtained by adding the appropriate estimates of

212   coefficients to the global mean and back-transforming through the above equations. For example,

213   the overall mean inside reserves $\mu_R$ for legal snapper was calculated as follows:

$$\mu_R = \left(1 - \frac{1}{1+e^{-(\gamma_0 + \gamma_1 \times \log(\lambda_R))}}\right) \times \lambda_R, \tag{7}$$

215   where the conditional mean count within reserves is $\lambda_R = e^{\beta_0 + R_{reserve}}$.

216

217                        **Parameterisation and prior distributions for model terms**

218          Let $A$ be a factor represented by a vector of coefficients $\boldsymbol{\beta} = (\beta_1, \ldots, \beta_\ell)$, where $\ell$ is the

219   number of levels in $A$. If the factor $A$ was fixed, coefficients $\beta_1$ to $\beta_{\ell-1}$ were each given prior

220   distributions

$$\beta \sim N(0,100). \tag{8}$$

222   A sum-to-zero constraint was used for fixed factors, such that one coefficient was set to

$$\beta_\ell = -\sum_{a=1}^{\ell-1} \beta_a. \tag{9}$$

224   For interactions between fixed and random factors, this constraint was also used for the fixed

225   factor within each level of the random factor. Components of variation for fixed factors were

226   defined as

$$\sigma_A^2 = \frac{\sum_{a=1}^{\ell} \beta_a^{\,2}}{\ell - 1}. \tag{10}$$

228   We shall refer to these as "variance components" in what follows, although for fixed factors these

229   are, strictly speaking, not variances but sums of squared fixed effects divided by the appropriate

230   degrees of freedom.

231          If $A$ was a random factor, the coefficients were given prior distributions

$$\beta \sim N(0, \sigma_A^2), \tag{11}$$

233   where $\sigma_A^2$ is common to all coefficients and represents the variance component for factor $A$. The

234   square roots of variance components for random factors were given standard half-Cauchy priors

235    (Gelman 2006). The dispersion parameter for models with the ZINB distribution was given the

236    prior distribution of

$$\delta \sim \text{Gamma}(0.0001, 0.0001). \tag{12}$$

238    For type 3 zero-inflated models, the parameters $\gamma_0$ and $\gamma_1$ were both given the prior distribution of

$$\gamma_0 , \gamma_1 \sim \text{Unif}(-5,5). \tag{13}$$

240    Code for fitting the selected models for both sublegal- and legal-sized snapper in R and

241    OpenBUGS are provided as a Supplement.

242

243                                  **RESULTS**

244            **Spatial factors: effect of reserve status and variation among locations and areas**

245             For legal snapper, reserve status was by far the greatest source of variation (Fig. 2).  After

246    controlling for variation among locations, areas, seasons, and years, the overall reserve effect (i.e.

247    the ratio of mean MaxN counts in reserve vs. non-reserve areas) was estimated to be 13.4 (see

248    Table 4 for uncertainty intervals). However, the reserve effect differed substantially among

249    locations, as evidenced by inclusion of the Reserve $\times$ Location interaction term in the model,

250    with the greatest effect observed at Leigh (effect size of 19.3), followed by Hahei (16.0) and then

251    Tawharanui (7.8). Estimated mean MaxN values per BUV deployment (mean relative densities)

252    in non-reserve areas were around 0.4 for both Leigh and Tawharanui and 0.2 for Hahei. In

253    protected areas, Leigh had by far the greatest mean relative density at 7.5, compared to ~3 in

254    Tawharanui and Hahei. In contrast, for sublegal snapper, reserve status was not included in the

255    chosen model at all. Instead, the two spatial factors (locations and areas) were most important for

256    determining the occurrence of excess zeros in sublegal snapper, with the smaller scale of areas

257    being most important (Fig. 2). For predicting the conditional mean count of sublegal snapper,

258    temporal factors were most important, and especially year. Densities of sublegal fish varied

259   among locations, however, with Leigh and Tawharanui supporting densities ~1.5 times that of

260   Hahei (Table 4).

261       At the finer spatial scale of areas, mean relative densities of sublegal snapper were similar

262   inside and outside reserves (Fig. 3). Credible intervals around the estimated means of areas were

263   too large to make strong conclusions about fine-scale spatial patterns. However, there was

264   potentially a gradient of increasing density from the western-most area (area 1) to Cape Rodney

265   (areas 9 and 10). At Tawharanui, there was little variation in estimated mean densities of sublegal

266   snapper among areas. At Hahei, the highest estimated mean density of sublegal snapper was that

267   from the central area of the reserve. For legal snapper, relative densities were consistently very

268   low outside of the reserves at all locations, and there was no apparent trend with proximity to the

269   reserve. The greatest densities of legal snapper were found in the central areas of the reserve at

270   Leigh (areas 5–6), with densities declining steeply toward the eastern and western boundaries of

271   the reserve. Within the reserves at Tawharanui and Hahei, however, there were gradients of

272   increasing density from east to west, and west to east, respectively. There did not appear to be

273   any consistent relationship between the densities of sublegal and legal snapper among areas,

274   except perhaps in non-reserve areas at Leigh, where similar spatial patterns were apparent for the

275   two size classes.

276       With regard to causal inferences, we wish to note in passing that the marine reserves in

277   the present study were established long before this monitoring program began, so a BACI-type

278   design (Underwood 1991), which would have provided stronger evidence for the causal effects of

279   the establishment of the marine reserves, was not possible. Thus, the estimated reserve effects

280   might be due to differences in the habitat or environment between the existing designated reserve

281   and non-reserves areas. However, our general conclusion that the differences observed were

282   caused by the absence of fishing in the reserves is supported by the fact that strong effects for

283    legal-sized snapper occurred in all three marine reserves, there was no spatial pseudo-replication

284    of the areas sampled at any of these locations, and no such reserve effects were observed for

285    sublegal-sized snapper.

286

287                    **Temporal factors: seasonal effects and variation among years**

288            Mean counts of sublegal- and legal-sized snapper were greater in autumn than in spring

289    (Table 5). The effect was strong for legal snapper and was the second most important source of

290    variation (Fig. 2), with an estimated seasonal effect size (ratio of densities in autumn vs. spring)

291    of 2.6. The overall effect was less convincing for sublegal snapper, with an estimated effect size

292    of 1.8 and a 95% credible interval that included 1. The models selected for both size classes

293    included interaction terms, indicating that the effect of season differed among years and locations

294    (Table 3). For both size classes, the seasonal effect was greater for Hahei than at other locations,

295    driven by relatively low densities in spring. There was little evidence of a strong seasonal effect

296    on sublegal fish at Tawharanui, but there was only one year in which this location was surveyed

297    in both seasons.

298            Annual variation was also important for both size classes (Fig. 2), with mean relative

299    densities varying substantially among the 12 years of the study (Fig. 4). The model for sublegal

300    snapper included an interaction between location and year, suggesting that different inter-annual

301    patterns were observed among locations. However, at all locations, the largest densities of

302    sublegal snapper were observed over the period from 1999 to 2001. Inter-annual patterns were

303    consistent among locations for legal snapper, as reflected by the absence of a location-by-year

304    interaction in the model for this size class. Autumnal densities of legal snapper within the

305    reserves at Leigh and Hahei appeared to peak in 2003 and decline thereafter (Fig. 4). The most

306    recent survey in 2010 at Hahei recorded the lowest autumnal density yet recorded at any location.

307  At Tawharanui, densities did not appear to vary substantially for the four years in which surveys

308  were done.

309

310                                    **DISCUSSION**

311                        **Effects of protection by marine reserves on snapper**

312            Marine reserve protection was by far the most important determinant of the relative

313  density of legal snapper, with the estimated component of variation associated with the reserve

314  effect being much greater than any of the other spatial or temporal factors (Fig. 2). When

315  averaged across all other factors, the relative density of legal snapper was estimated to be 13

316  times greater inside reserves than outside reserves (Table 4), a similar result to the value of 14

317  times greater, which was reported from an analysis of the first three years of this monitoring

318  program (Willis et al. 2003a).

319            Our results indicated large differences in the effects of reserves on legal snapper among

320  locations, which were not reported by Willis et al. (2003a). Differences in reserve effects have

321  also been observed in a recent study of another species (rock lobster *Jasus edwardsii*) in a set of

322  reserves which included the three studied here (Freeman et al. 2012). The largest effect for legal

323  snapper was observed at Leigh, with densities estimated to be nearly 20 times greater within the

324  reserve than outside the reserve, while Tawharanui and Hahei had effect sizes of 8 and 16,

325  respectively. This range in effect sizes compares favourably also with those estimated from the

326  Poor Knights Islands Marine Reserve, located offshore within the same bioregion, where

327  densities of legal-sized snapper were estimated to be 22 and 11 times greater than those at

328  comparable non-reserve locations (Denny et al. 2004). The densities of legal snapper outside the

329  reserves at Leigh and Tawharanui were roughly the same (Table 4), which is not surprising, given

330  their close proximity and similar environmental conditions. However, the density within the

331     reserve at Leigh was over twice that of the reserves at Tawharanui and Hahei, which were

332     similar.

333         There are several potential factors that might explain differences in the measured effect

334     sizes of marine reserves placed in different locations. Firstly, theory suggests that the size of a

335     reserve is an important factor determining the extent of the recovery of populations within a

336     reserve (e.g. Kramer & Chapman 1999). Yet, results from recent meta-analyses examining the

337     relationship between the size of the reserve and its effects on populations have been mixed: a

338     positive relationship was evident in some studies (Claudet et al. 2008, Stewart et al. 2009) but not

339     in others (Halpern 2003, Lester et al. 2009). Generally speaking, the effects of reserve size must

340     be considered in light of the home-range dynamics of a species, as this will influence the

341     proportion of fish that will move into adjacent fished areas (Kramer & Chapman 1999, Moffitt et

342     al. 2009). The spatial dynamics of snapper are complex, as this species shows considerable

343     variation in movement patterns among individuals. Tagging studies of snapper in this region have

344     shown that some snapper make seasonal inshore-offshore migrations, travelling up to tens or

345     even hundreds of km, while others are resident on reefs and move only hundreds of metres

346     (Crossland 1976, Willis et al. 2001, Parsons et al. 2003, 2010, 2011, Egli & Babcock 2004).

347     Summertime onshore migration of fish that subsequently become resident on inshore reefs is

348     thought to be an important mechanism responsible for increases in densities of adult snapper

349     within reserves (Willis et al. 2001, Willis et al. 2003a, Denny et al. 2004, Willis & Millar 2005).

350     The position of reserves with respect to patterns of onshore migration in this species is therefore

351     likely to be an important factor in determining their success. Patterns of settlement of larvae in

352     the vicinity of reserves could also potentially influence densities of sublegal- and legal-sized

353     snapper in reserves, but post-settlement processes such as mortality and dispersal are likely to

354     moderate the influence of larval supply on adult densities (Freeman et al. 2012). The colonisation

355    of reserves by seasonal migrants potentially allows the number of resident adult snapper to

356    accumulate more rapidly than would be possible through the progression of juvenile fish to

357    adulthood (as documented at the nearby Poor Knights Islands Marine Reserve by Denny et al.

358    2004), provided the reserve is large enough to protect them once they are resident. Drawing on

359    knowledge from tagging studies of snapper in the vicinity of Leigh and Tawharanui, a recent

360    simulation study concluded that both the Leigh and Tawharanui reserves were of insufficient size

361    to restore densities to unfished levels (Babcock et al. 2012). Thus, the size of the reserves may

362    well be an important factor contributing to the differential reserve effects shown here. Densities

363    of sublegal snapper, and legal snapper outside reserves, were similar at Leigh and Tawharanui

364    (Table 4). Yet, densities of legal snapper were much greater in the larger reserve at Leigh. Legal

365    snapper in the Hahei reserve had a mean density similar to that of the Tawharanui reserve, despite

366    this location having much lower densities of sublegal snapper and legal snapper outside the

367    reserve, consistent with the general southward decrease in the abundance of this species. This

368    could be due to the reserve at Hahei being much larger than the other two and, perhaps more

369    importantly (Freeman et al. 2012), having more than twice the offshore extent (Table 1). These

370    patterns are consistent with the hypothesis that the size of the reserves plays a key role in

371    producing the observed variation in their effects.

372        Secondly, several recent meta-analyses have demonstrated a positive relationship between

373    the duration of protection and the effect size of marine reserves (Micheli et al. 2004, Claudet et

374    al. 2008, Molloy et al. 2009). If reserve age was an important factor in this study, a trend of

375    increasing density over time inside these reserves would be expected, yet no such trend was

376    present in these data (Fig. 4). While the reserve at Leigh, the oldest of the three reserves studied

377    here (Table 1), showed the greatest effect size, it is only four years older than the one at

378    Tawharanui which showed a markedly smaller effect. One might also expect greater densities in

379  the reserve at Tawharanui than the one at Hahei, being 11 years older (Table 1), but they were in

380  fact very similar (Table 4). Thus, differences in the ages of the reserves do not appear to

381  contribute substantially to the differential effect sizes seen here.

382       A third group of variables potentially responsible for differential effects of marine

383  reserves includes differences in environmental conditions and habitat at these locations (García-

384  Charton et al. 2004, Huntington et al. 2010). Environmental conditions such as water clarity,

385  sedimentation levels, wind fetch, and wave exposure are broadly similar among the locations

386  studied here (Appendix B in Shears et al. 2008). The speed of the local current could potentially

387  influence the distance covered by the bait plume, and thus the number of fish drawn to a BUV,

388  but we consider it unlikely that general current regimes varied significantly among the locations

389  studied. Differences in habitat among locations are more likely to have contributed to the

390  differences observed in this study. Seasonal inshore migrants will presumably be more likely to

391  remain as residents on reefs that are of sufficient size and quality. Moreover, less favourable

392  habitat is expected to support lower densities, as fish would be required to move over greater

393  areas in order to satisfy their nutritional needs, therefore putting them at greater risk of moving

394  outside of the reserve and into fished areas. The reserves at which the strongest effects were

395  observed, Leigh and Hahei, contain more extensive reefs than at Tawharanui, and include

396  features such as islands (providing shelter and shallow zones) and vertical reef walls. Indeed, the

397  largest densities at Leigh were observed in the central areas of the reserve where these features

398  are located, although larger densities of targeted fish at the centre of a reserve are expected in any

399  event due to the increased risk of them exiting the reserve in areas nearer its borders (Kramer &

400  Chapman 1999).

401       Finally, differential levels of fishing effort at these locations may also contribute to the

402  differential reserve effects in many ways. Fishing effort in nearby non-reserve areas is likely to

403    be similar among these locations, all of which are very popular with recreational fishers. It has

404    been suggested that more illegal fishing may occur within the reserve at Tawharanui than at

405    Leigh (Babcock et al. 2012). Poor enforcement is thought to be a major issue potentially

406    compromising the effectiveness of marine reserves in many regions of the world (Guidetti et al.

407    2008). Thus, a lack of compliance to the no-take status may therefore contribute to the relatively

408    modest estimated effect of the reserve at Tawharanui. Commercial fishing, which occurs

409    primarily offshore, might also potentially moderate the numbers of fish available to make the

410    seasonal inshore migration.

411            We suggest that variation in the estimated effects of these three reserves is likely caused

412    by a combination of factors, including size, habitat, the degree of compliance with their no-take

413    status, and patterns of inshore migration. Environmental planners need to consider these factors

414    carefully when planning future marine reserves. Perhaps the most important point is that variation

415    in the effects of reserves exists and should be expected, even within the same geographic region.

416    The sources of such variation in snapper clearly require further study.

417

418                    **Temporal and spatial variation in snapper**

419            Other than the reserve effect, temporal factors (season and year) were generally more

420    important than the other spatial factors for predicting relative densities of snapper in this study. In

421    particular, the seasonal effect was strong (Fig. 2), with counts in autumn being ~ 2–3 times

422    greater than those in spring (Table 5, Fig. 3, Fig. 4). Seasonal changes in inshore snapper

423    numbers has been documented in many other studies of this species in this region, and is thought

424    to be a result of inshore migration for spawning (Francis 1995, Millar et al. 1997, Millar & Willis

425    1999, Willis et al. 2003a, Willis & Millar 2005). This explanation is consistent with a stronger

426    seasonal effect for legal than sublegal snapper, as found here, because fewer sublegal fish will be

427  reproductively active. The seasonal effect was variable among years and locations, supporting the

428  results of Francis (1995). The effect was notably absent from Tawharanui for sublegal snapper,

429  and was strongest at Hahei for both size classes. Although Willis & Millar (2005) found that the

430  seasonal effect for legal snapper was different inside versus outside the marine reserves, no such

431  interaction was apparent in the present analysis. This is due to differences in the structure of the

432  statistical models: Willis & Millar (2005) used an additive identity-link function as opposed to

433  the log-link model presented here. Thus, an interaction may exist on an additive scale, but not a

434  multiplicative scale.

435        For sublegal snapper, the effects of the spatial factors on the overall density were difficult

436  to interpret because they were split between separate predictors for the excess zeros and the

437  counts, an unfortunate property of this type of zero-inflated model (Smith et al. 2012). However,

438  the pattern of excess zeros was apparently driven by spatial rather than temporal factors, and at

439  the finer spatial scale of individual areas in particular (Fig. 2). This indicates that some areas are

440  consistently more likely than others to give counts of zero for sublegal snapper, perhaps due to

441  spatial variation in the suitability of habitat or environmental conditions among areas and

442  locations (Francis 1995, Ross et al. 2007).

443        Inter-annual variation in both size classes was relatively large (Fig. 2), which is consistent

444  with studies showing highly variable recruitment in this species, related to temperature (Francis

445  1993) or prevailing wind patterns (Zeldis et al. 2005). There were peaks in the relative densities

446  of sublegal snapper in 1999–2001, and of legal snapper in around 2003. Considering the growth

447  curve for this species (Millar et al. 1999), this may correspond to a strong recruitment pulse

448  observed in the mid-1990s (Maunder & Starr 2001) which then boosted densities of legal fish in

449  reserves in the early 2000s. In years subsequent to 2003, a trend was observed that suggests that

450  snapper densities declined inside reserves. Although these inter-annual patterns may reflect

451    region-wide temporal changes in snapper populations, they might also to some extent be caused

452    by changes in the personnel conducting the monitoring from year to year. Nonetheless, it is clear

453    that any attempts to understand temporal trends and make accurate estimates of the effects of

454    reserves or seasons require that reserves be monitored consistently over several years.

455

456                                    **Concluding remarks**

457          Here, we demonstrated the use of Bayesian zero-inflated generalised linear mixed models

458    for simultaneously quantifying the effects of marine reserves and variation associated with a

459    number of spatial and temporal factors, including three locations divided into 26 areas, two

460    seasons, and multiple years, in an unbalanced design. The Bayesian approach easily

461    accommodated the hierarchical sampling designs and mixture of fixed and random effects and

462    their interactions in an ANOVA-type analysis, while also incorporating various nonstandard error

463    distributions to account for overdispersion and excess zeros, which are a common issue in

464    ecology (see also Smith et al. 2012). Using the output from the MCMC, it was straightforward to

465    estimate effect sizes of interest while accounting for the other factors. The results obtained by our

466    models were generally consistent with those published earlier for this species, with the distinction

467    that interaction terms were also apparent in our models, indicating important variation in the

468    effects of reserves in time and space and at a variety of scales. Rigorous estimates of (and

469    credible intervals for) components of variation attributable to different sources of variation,

470    expressed as the estimated standard deviation among the levels of each factor (Fig. 2), were a

471    particularly useful output from our analysis. Following Gelman et al. (2005), components of

472    variation were calculated for both fixed and random factors so that the relative contribution of all

473    factors and their interactions could be directly compared. This allowed us to ascertain the most

474    important factors for explaining variation in counts of snapper, which complemented the

475    estimation of the effects of interest. The results herein have a wide range of potential benefits,

476    including greater understanding of the interplay between the effects of management and spatial

477    and temporal ecological patterns, the provision of valuable data for stochastic simulation models

478    of ecosystems, and enabling more accurate predictions for future reserves.

479         While classical approaches to estimating effect sizes and components of variation in

480    mixed models have been used for many years in ecological studies (Lewis Jr. 1978, Underwood

481    & Chapman 1996, Underwood 1997, Anderson & Millar 2004), many authors have noted

482    advantages of the Bayesian approach over its classical counterparts (Ellison 1996, 2004, Clark

483    2005, Cressie et al. 2009). We refer readers to the recent work of Bolker et al. (2009, 2013) for

484    general comparisons and guidelines for a range of methods for fitting generalised linear mixed

485    models, and Link et al. (2002) for a more directed discussion of the advantages of MCMC and

486    the Bayesian approach. The present study highlights a particular advantage of contemporary

487    Bayesian software (e.g. OpenBUGS), in that it provides modellers with the flexibility to develop

488    new and innovative model structures, such as the linked zero-inflated model used here (Smith et

489    al. 2012). We note that elements of the dataset used here made it particularly well-suited to

490    modelling with Bayesian MCMC, such as the highly unbalanced design, the presence of multiple

491    fixed and random effects, and the need for nonstandard error distributions to account for

492    overdispersion and excess zeros. Simultaneously incorporating all these features in a single

493    model using any other approach would be very challenging. Yet, such complexities are common

494    in monitoring data, and should not be overlooked. More generally, we consider that our approach

495    provides a useful and flexible framework for placing the effects of management actions, such as

496    protection by marine reserves, into a broader context of natural underlying variation in biological

497    systems.

498

505

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687

688                                **SUPPLEMENTAL MATERIAL**

689  *Supplement***:** R and OpenBUGS code and datasets for fitting Bayesian zero-inflated mixed

690  models to counts of sublegal- and legal-sized snapper from a marine reserve monitoring program.

691

692    Table 1. Details regarding the age and size of each of the three marine reserves examined in this

693    study.

694

| Marine reserve | Year established | Area (ha) | Approx. coastal extent (m) | Approx. offshore extent (m) |
|---|---|---|---|---|
| Cape Rodney-Okakari Point (Leigh) | 1977[1] | 518 | 5,240 | 800 |
| Tawharanui | 1981 | 350 | 3,200 | 800 |
| Te Whanganui-A-Hei (Hahei) | 1992 | 840 | 3,740 | 1,850 |

695

696    [1]Note that some sources have given the date of establishment for this reserve as 1975. In their

697    original description of the reserve, Ballantine and Gordon (1979) indicate that it was legally

698    established in 1975, but was officially opened and became operational in 1977.

699

700     Table 2. The number of baited underwater video (BUV) sampling units obtained in each year,

701     season and location. Samples within each survey were allocated to reserve and non-reserve areas

702     equally in most cases.

703

| Year | Leigh Autumn | Leigh Spring | Tawharanui Autumn | Tawharanui Spring | Hahei Autumn | Hahei Spring |
|------|--------|--------|--------|--------|--------|--------|
| 1997 | - | 48 | - | 24 | - | 27 |
| 1998 | 48 | 48 | 24 | 24 | 30 | 25 |
| 1999 | 48 | - | 24 | - | 30 | - |
| 2000 | 47 | 43 | - | - | 30 | 30 |
| 2001 | 48 | 47 | - | - | 26 | 30 |
| 2002 | 48 | - | - | - | - | - |
| 2003 | 48 | - | - | - | 30 | - |
| 2004 | - | - | - | - | - | 30 |
| 2005 | 48 | - | - | - | - | - |
| 2006 | - | - | - | - | 30 | - |
| 2007 | 48 | - | 32 | - | - | - |
| 2010 | - | - | - | - | 30 | - |

704

705 Table 3. Sources of variation for the full ANOVA model, based all factors in the study design.

706 The terms that were not included as candidates for model selection, based on preliminary

707 heuristics, are indicated with an asterisk. The abbreviation for each term, as shown, was used to

708 indicate the model parameters associated with that term in the GLMs, given in equations (3)–(5)

709 in the text. Terms that were chosen to be included in the final models of relative densities of legal

710 or sublegal snapper, obtained using model selection on the basis of the DIC, are also provided.

711

| Source of variation | Abbreviation | Degrees of Freedom | Fixed or random | Selected for sublegal (S) or legal (L) models |
|---|---|---|---|---|
| Reserve | *R* | 1 | Fixed | L |
| Season | *S* | 1 | Fixed | S L |
| Location | *L* | 2 | Fixed | S L |
| Year | *Y* | 11 | Random | S L |
| Area (nested in *L×R*) | *A* | 20 | Random | S L |
| Reserve×Season | *RS* | 1 | Fixed | |
| Reserve×Location | *RL* | 2 | Fixed | L |
| Reserve×Year | *RY* | 11 | Random | L |
| Season×Location | *SL* | 2 | Fixed | S L |
| Season×Year | *SY* | 2 | Random | S L |
| Season×Area (nested in *L×R*) | *SA* | 18 | Random | |
| Location×Year | *LY* | 8 | Random | S |
| Year×Area (nested in *L×R*) | *YA* | 124 | Random | |

| | | | |
|---|---|---|---|
| Reserve×Season×Location | *RSL* | 2 | Fixed |
| Reserve×Season×Year | *RSY* | 2 | Random |
| Reserve×Location×Year | *RLY* | 8 | Random |
| Season×Location×Year* | *SLY* | 8 | Random |
| Season×Year×Area (nested in *L×R*)* | *SYA* | 28 | Random |
| Reserve×Season×Year×Location* | *RSYL* | 2 | Random |

712    Table 4. Point estimates (mean of the posterior distribution, represented by the set of values given

713    by MCMC) and 95% credible intervals (0.025 and 0.975 quantiles of the posterior distribution) of

714    the mean relative densities for either sublegal or legal snapper in reserve and non-reserve areas at

715    each of three locations. Reserve and non-reserve densities for sublegal snapper were pooled

716    because there was no reserve effect in the model. Estimates of the ratio of reserve to non-reserve

717    densities are also provided for legal snapper as an index of the 'reserve effect'. The point

718    estimates for the ratios were obtained by first calculating the ratios for each MCMC iteration,

719    taking the natural log of the ratios, calculating the mean, and then back-transforming.

720

| Location | Sublegal | Legal | | |
|---|---|---|---|---|
| | Non-reserve and Reserve | Non-reserve | Reserve | Ratio R:NR |
| Leigh | 3.08 (1.97, 4.46) | 0.40 (0.17, 0.74) | 7.49 (4.42, 12.09) | 19.34 (8.76, 44.18) |
| Tawharanui | 3.34 (1.81, 5.63) | 0.41 (0.15, 0.84) | 3.05 (1.40, 5.48) | 7.77 (2.98, 22.06) |
| Hahei | 1.79 (0.97, 2.88) | 0.19 (0.06, 0.42) | 2.89 (1.26, 5.48) | 16.02 (5.37, 50.76) |
| All reserves | 2.67 (1.8, 3.73) | 0.30 (0.15, 0.50) | 3.98 (2.49, 5.92) | 13.43 (7.43, 25.48) |

721

722

723 Table 5. Point estimates and 95% credible intervals (as described in the legend for Table 4) of the mean relative densities for either legal

724 or sublegal snapper in each of two seasons at each of three locations. Estimates for ratios of seasonal effects were obtained as described

725 for reserve effects in the caption for Table 4.

726

|  | Sublegal | | | Legal | | |
|---|---|---|---|---|---|---|
|  | Spring | Autumn | Ratio A:S | Spring | Autumn | Ratio A:S |
| Leigh | 2.49 (1.38, 3.99) | 4.48 (2.67, 6.69) | 1.81 (0.99, 3.16) | 1.35 (0.67, 2.34) | 2.65 (1.56, 4.08) | 2.01 (1.07, 3.96) |
| Tawharanui | 2.91 (1.12, 5.9) | 3.06 (1.68, 5.37) | 1.11 (0.49, 2.44) | 0.73 (0.28, 1.41) | 1.8 (0.91, 3.09) | 2.54 (1.16, 6.1) |
| Hahei | 1.18 (0.62, 2.01) | 3.45 (2.05, 5.25) | 2.97 (1.62, 5.35) | 0.43 (0.16, 0.85) | 1.39 (0.71, 2.37) | 3.35 (1.67, 7.33) |
| All reserves | 1.96 (0.97, 3.27) | 3.37 (2.18, 4.94) | 1.76 (0.98, 3.12) | 0.74 (0.37, 1.24) | 1.86 (1.14, 2.74) | 2.55 (1.35, 5.15) |

727

728

729 **FIGURE CAPTIONS**

730 Fig. 1. A map showing the locations of three marine reserves in north-eastern New Zealand

731 (upper left panel). Also shown are the individual numbered areas (fine lines and numbers), and

732 marine reserves (bold lines) at each location, as indicated. Note that the borders of Tawharanui

733 Marine Reserve were moved slightly in September 2011 and are now different to those shown

734 here.

735

736 Fig. 2. A variance components plot (Gelman 2005) showing the variation associated with each

737 term in the chosen models, expressed as the estimate of the standard deviation σ among levels,

738 for predicting the relative density of legal or sublegal snapper. For the latter, separate linear

739 predictors were used to model the probability of an excess zero ($\pi$) and the conditional mean of

740 the counts ($\lambda$), so a separate panel is used for each. Point estimates (means of posterior

741 distributions) are represented by vertical lines, with 50% and 95% credible intervals for the

742 means as thick and thin horizontal lines, respectively.

743

744 Fig. 3. Fine-scale spatial patterns in the estimated mean relative density of sublegal (triangles)

745 and legal (circles) snapper, in areas within three locations. Open and closed symbols represent the

746 point estimates (means of posterior distributions) for spring and autumn, respectively. Error bars

747 are 95% credible intervals for the means.

748

749 Fig. 4. Inter-annual and season patterns in the estimated mean relative density of sublegal

750 (triangles) and legal (circles) snapper at three locations. Open and closed symbols represent the

751 point estimates (means of posterior distributions) for spring and autumn, respectively. Error bars

752 are 95% credible intervals for the means. For legal snapper, estimates for within the reserves only

753    are shown, because too few snapper were observed outside the reserves to show any interpretable

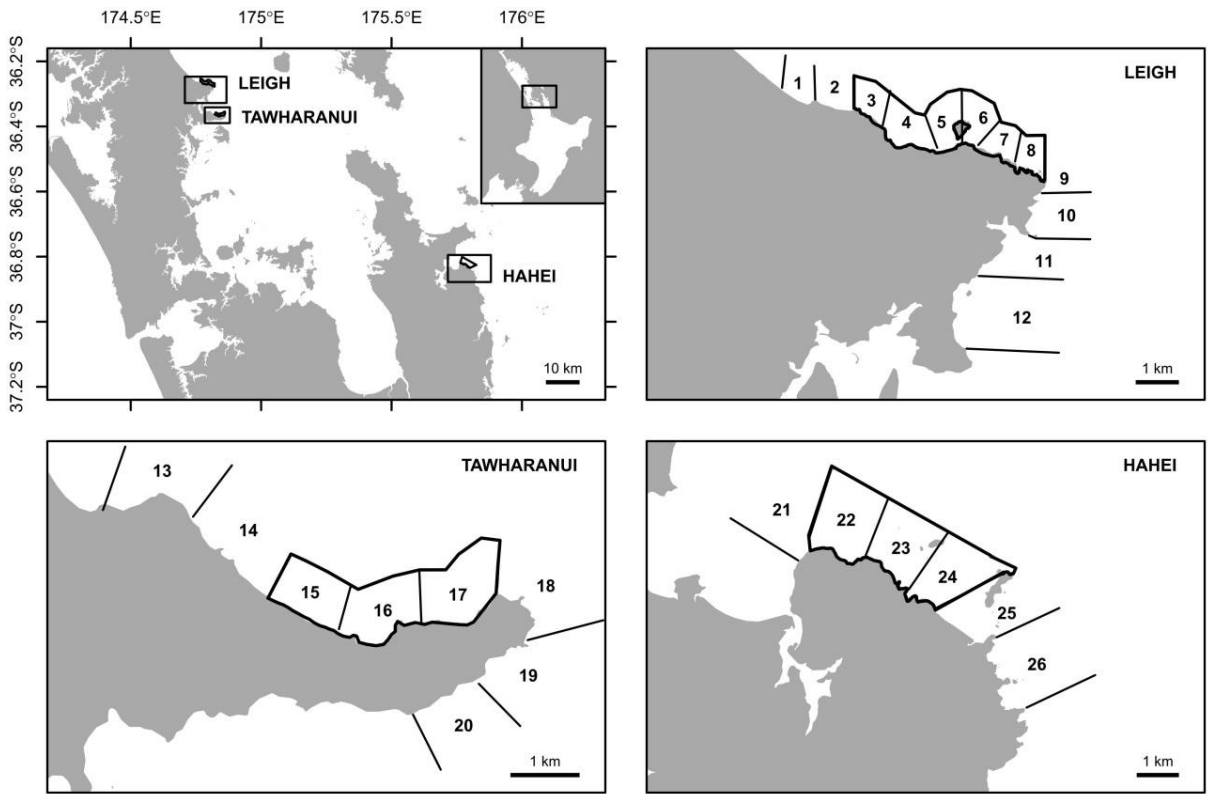754    patterns. Note that the scale of the *y*-axes varies differ for sublegal (left) and legal (right) panels.
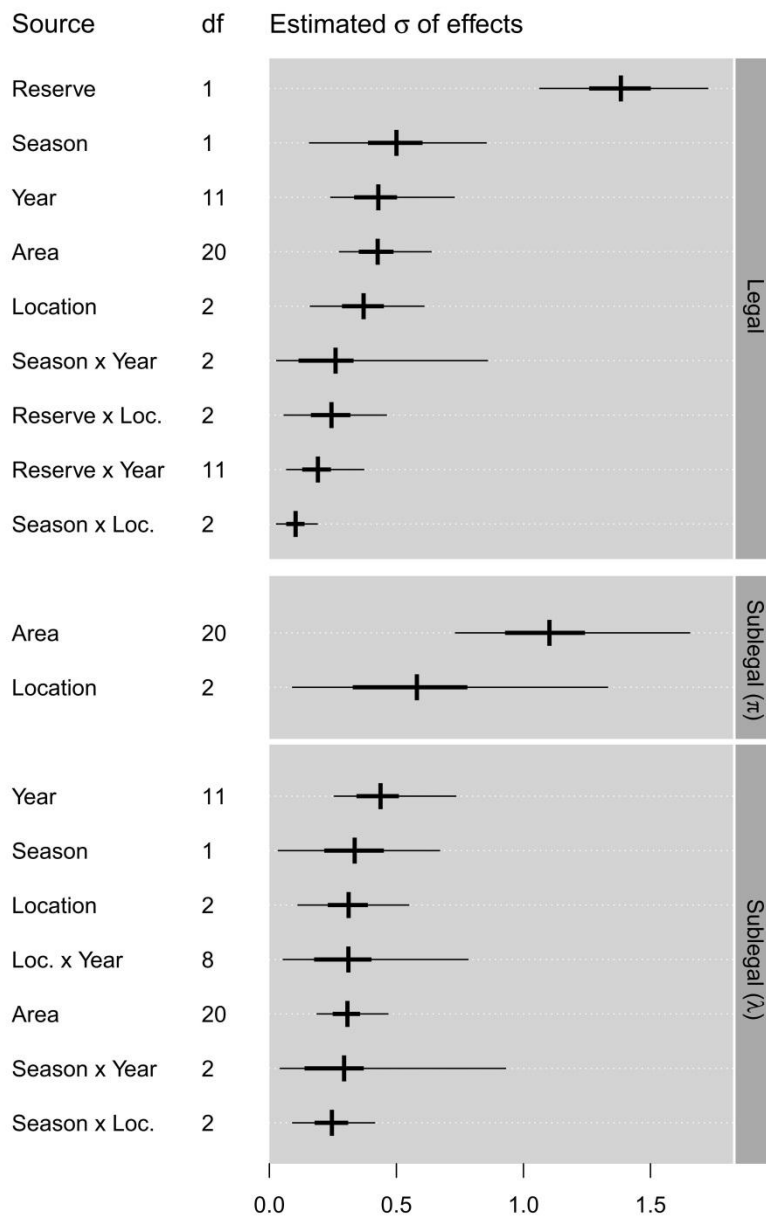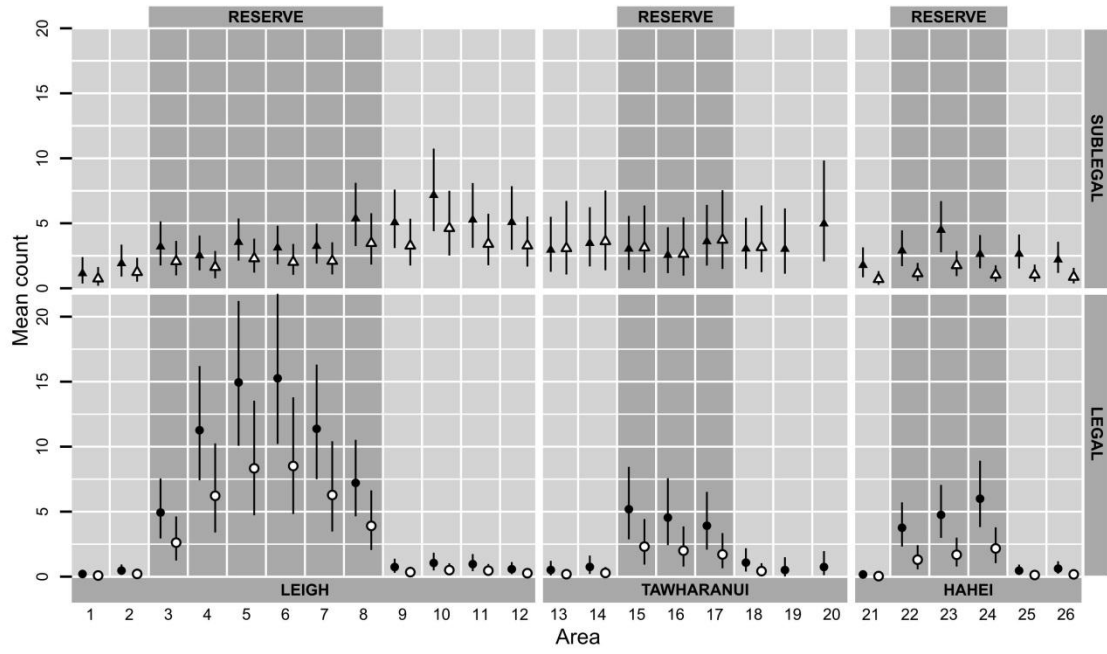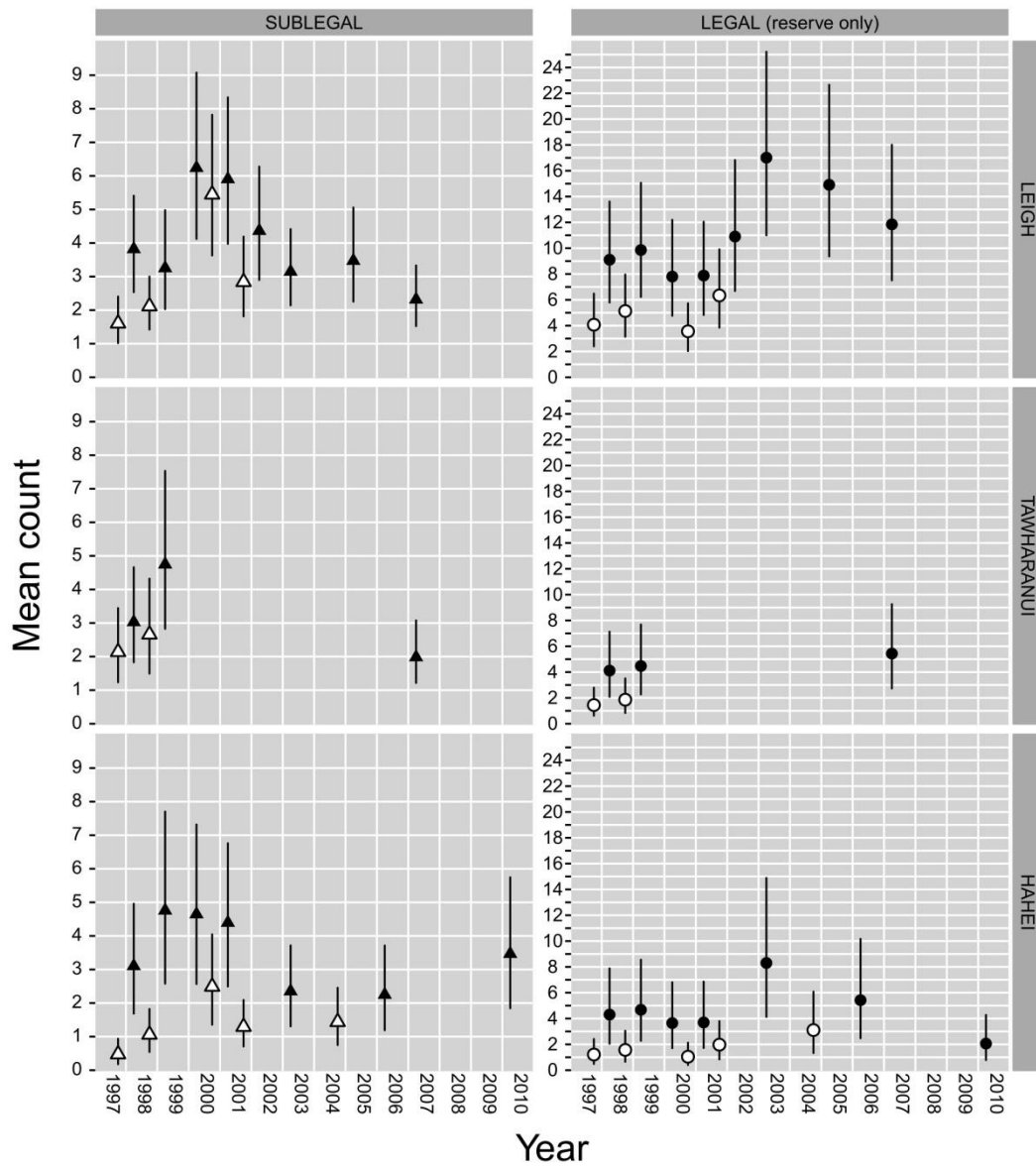
Fig. 1

Fig. 2

Fig. 3

Fig. 4