

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

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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

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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.

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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

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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.

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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.

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Candidate models and model selection

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Counts of sublegal and legal snapper from the monitoring program were analysed using
Bayesian zero-inflated generalised linear mixed models (GLMMs). Following Gelman (2005),
we used the Bayesian approach to model variation associated with the effects of marine reserves,
as well as seasons, locations, areas, and years, in a structured analysis-of-variance (ANOVA)
framework. The term ANOVA is used here to refer specifically to the structuring of the
coefficients into ‘batches’, so that the levels of each categorical factor are grouped together.
Variance components are estimated for each batch of coefficients in order to compare the relative
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 λ , the mean of the Poisson distribution
165 conditional on the absence of excess zero, and π , the probability of the occurrence of an excess

166 zero. In addition, the ZINB had the parameter δ which allowed for aggregation (overdispersion)
167 in the counts. For either of these error distributions, the overall mean is given by

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

169 The conditional mean, λ , was modelled as a linear predictor of candidate terms with a log-
170 link function. Zero inflation, π , 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 α 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 λ , and also π 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 π .

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.

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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:

$$196 \quad y_{hijklm} \sim \text{ZINB}(\lambda_{hijkl}, \pi_{hijkl}, \delta). \quad (2)$$

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

$$198 \quad \log(\lambda_{hijkl}) = \beta_0 + S_i + L_j + A_{k(j)} + Y_l + (SL)_{ij} + (SY)_{il} + (LY)_{jl} \quad (3)$$

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

$$200 \quad \log\left(\frac{\pi_{hijkl}}{1-\pi_{hijkl}}\right) = \beta_0^{(\pi)} + L_j^{(\pi)} + A_{k(j)}^{(\pi)}. \quad (4)$$

201 For legal-sized snapper, the linear predictor for λ was

$$202 \quad \log(\lambda_{hijkl}) = \beta_0 + R_h + S_i + L_j + A_{k(h \times j)} + Y_l + (RL)_{hj} + (RY)_{hl} + (SL)_{ij} + (SY)_{il} \quad (5)$$

203 and the model for the zero inflation parameter was

$$204 \quad \log\left(\frac{\pi_{hijkl}}{1-\pi_{hijkl}}\right) = \gamma_0 + \gamma_1 \log(\lambda_{hijkl}) \quad (6)$$

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), β_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 λ and π 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 μ_R for legal snapper was calculated as follows:

$$214 \quad \mu_R = \left(1 - \frac{1}{1 + e^{-(\gamma_0 + \gamma_1 \times \log(\lambda_R))}}\right) \times \lambda_R, \quad (7)$$

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

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

218 Let A be a factor represented by a vector of coefficients $\boldsymbol{\beta} = (\beta_1, \dots, \beta_\ell)$, where ℓ is the
 219 number of levels in A . If the factor A was fixed, coefficients β_1 to $\beta_{\ell-1}$ were each given prior
 220 distributions

$$221 \quad \beta \sim N(0, 100). \quad (8)$$

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

$$223 \quad \beta_\ell = -\sum_{a=1}^{\ell-1} \beta_a. \quad (9)$$

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

$$227 \quad \sigma_A^2 = \frac{\sum_{a=1}^{\ell} \beta_a^2}{\ell-1}. \quad (10)$$

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

$$232 \quad \beta \sim N(0, \sigma_A^2), \quad (11)$$

233 where σ_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

$$237 \quad \delta \sim \text{Gamma}(0.0001, 0.0001). \quad (12)$$

238 For type 3 zero-inflated models, the parameters γ_0 and γ_1 were both given the prior distribution of

$$239 \quad \gamma_0, \gamma_1 \sim \text{Unif}(-5, 5). \quad (13)$$

240 Code for fitting the selected models for both sublegal- and legal-sized snapper in R and
241 OpenBUGS are provided as a Supplement.

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RESULTS

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

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For legal snapper, reserve status was by far the greatest source of variation (Fig. 2). After controlling for variation among locations, areas, seasons, and years, the overall reserve effect (i.e. the ratio of mean MaxN counts in reserve vs. non-reserve areas) was estimated to be 13.4 (see Table 4 for uncertainty intervals). However, the reserve effect differed substantially among locations, as evidenced by inclusion of the Reserve \times Location interaction term in the model, with the greatest effect observed at Leigh (effect size of 19.3), followed by Hahei (16.0) and then Tawharanui (7.8). Estimated mean MaxN values per BUV deployment (mean relative densities) in non-reserve areas were around 0.4 for both Leigh and Tawharanui and 0.2 for Hahei. In protected areas, Leigh had by far the greatest mean relative density at 7.5, compared to ~ 3 in Tawharanui and Hahei. In contrast, for sublegal snapper, reserve status was not included in the chosen model at all. Instead, the two spatial factors (locations and areas) were most important for determining the occurrence of excess zeros in sublegal snapper, with the smaller scale of areas being most important (Fig. 2). For predicting the conditional mean count of sublegal snapper, 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.

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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.

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DISCUSSION

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Effects of protection by marine reserves on snapper

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Marine reserve protection was by far the most important determinant of the relative density of legal snapper, with the estimated component of variation associated with the reserve effect being much greater than any of the other spatial or temporal factors (Fig. 2). When averaged across all other factors, the relative density of legal snapper was estimated to be 13 times greater inside reserves than outside reserves (Table 4), a similar result to the value of 14 times greater, which was reported from an analysis of the first three years of this monitoring program (Willis et al. 2003a).

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Our results indicated large differences in the effects of reserves on legal snapper among locations, which were not reported by Willis et al. (2003a). Differences in reserve effects have also been observed in a recent study of another species (rock lobster *Jasus edwardsii*) in a set of reserves which included the three studied here (Freeman et al. 2012). The largest effect for legal snapper was observed at Leigh, with densities estimated to be nearly 20 times greater within the reserve than outside the reserve, while Tawharanui and Hahei had effect sizes of 8 and 16, respectively. This range in effect sizes compares favourably also with those estimated from the Poor Knights Islands Marine Reserve, located offshore within the same bioregion, where densities of legal-sized snapper were estimated to be 22 and 11 times greater than those at comparable non-reserve locations (Denny et al. 2004). The densities of legal snapper outside the reserves at Leigh and Tawharanui were roughly the same (Table 4), which is not surprising, given 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 un-fished 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

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506

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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 ¹Note 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		Tawharanui		Hahei	
	Autumn	Spring	Autumn	Spring	Autumn	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	<i>R</i>	1	Fixed	L
Season	<i>S</i>	1	Fixed	S L
Location	<i>L</i>	2	Fixed	S L
Year	<i>Y</i>	11	Random	S L
Area (nested in $L \times R$)	<i>A</i>	20	Random	S L
Reserve \times Season	<i>RS</i>	1	Fixed	
Reserve \times Location	<i>RL</i>	2	Fixed	L
Reserve \times Year	<i>RY</i>	11	Random	L
Season \times Location	<i>SL</i>	2	Fixed	S L
Season \times Year	<i>SY</i>	2	Random	S L
Season \times Area (nested in $L \times R$)	<i>SA</i>	18	Random	
Location \times Year	<i>LY</i>	8	Random	S
Year \times Area (nested in $L \times R$)	<i>YA</i>	124	Random	

Reserve×Season×Location	<i>RSL</i>	2	Fixed
Reserve×Season×Year	<i>RSY</i>	2	Random
Reserve×Location×Year	<i>RLY</i>	8	Random
Season×Location×Year*	<i>SLY</i>	8	Random
Season×Year×Area (nested in $L\times R$)*	<i>SYA</i>	28	Random
Reserve×Season×Year×Location*	<i>RSYL</i>	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

FIGURE CAPTIONS

729

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 (π) and the conditional mean of
740 the counts (λ), 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.

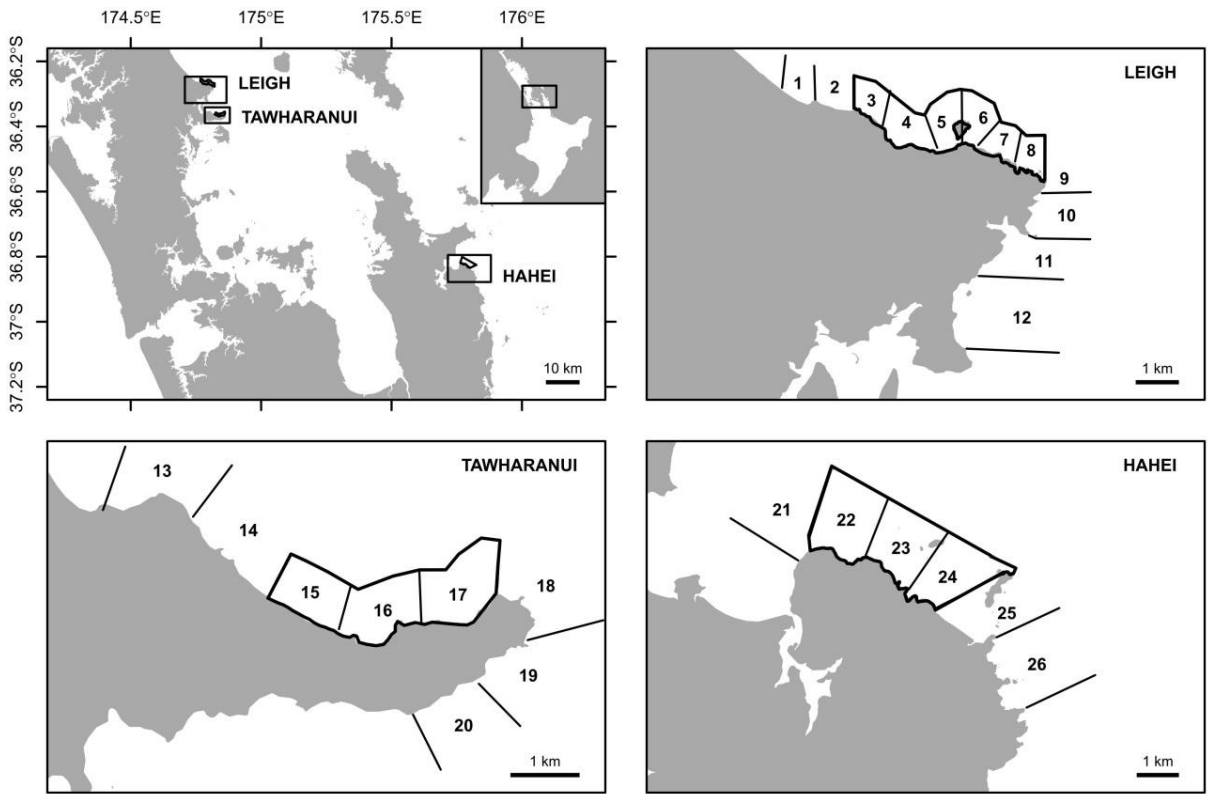


Fig. 1

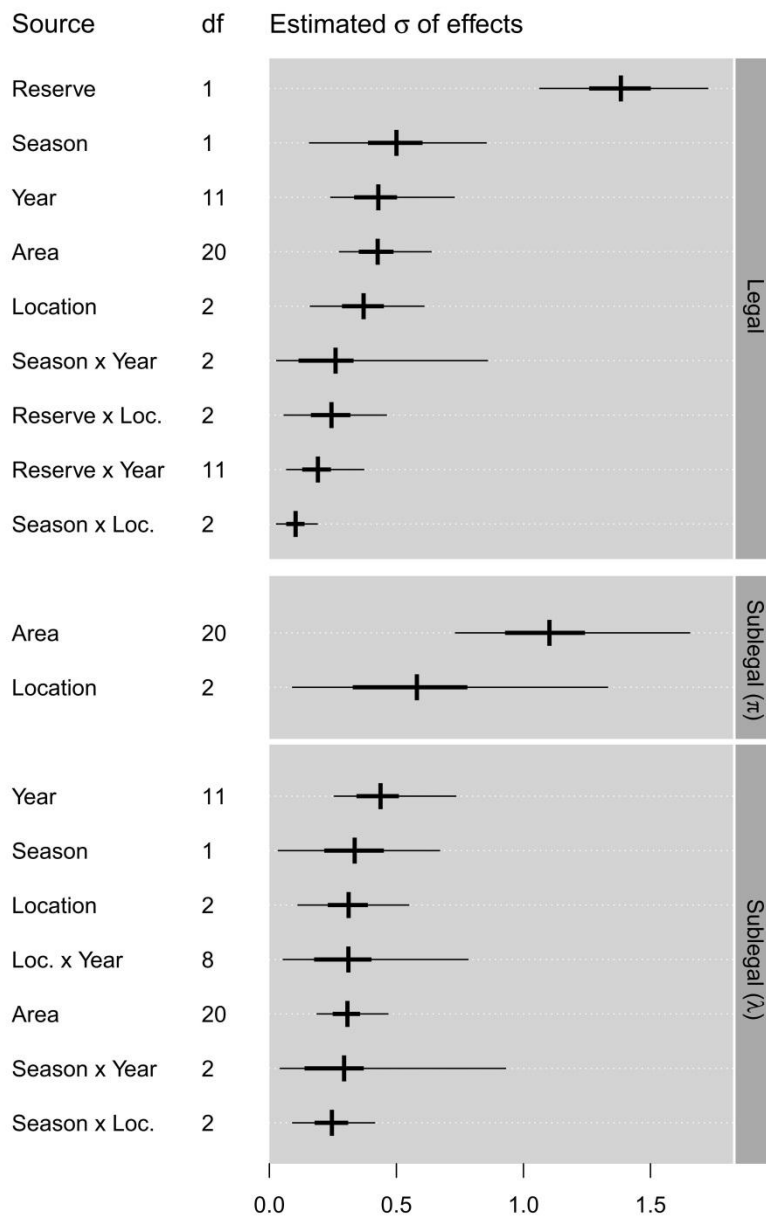


Fig. 2

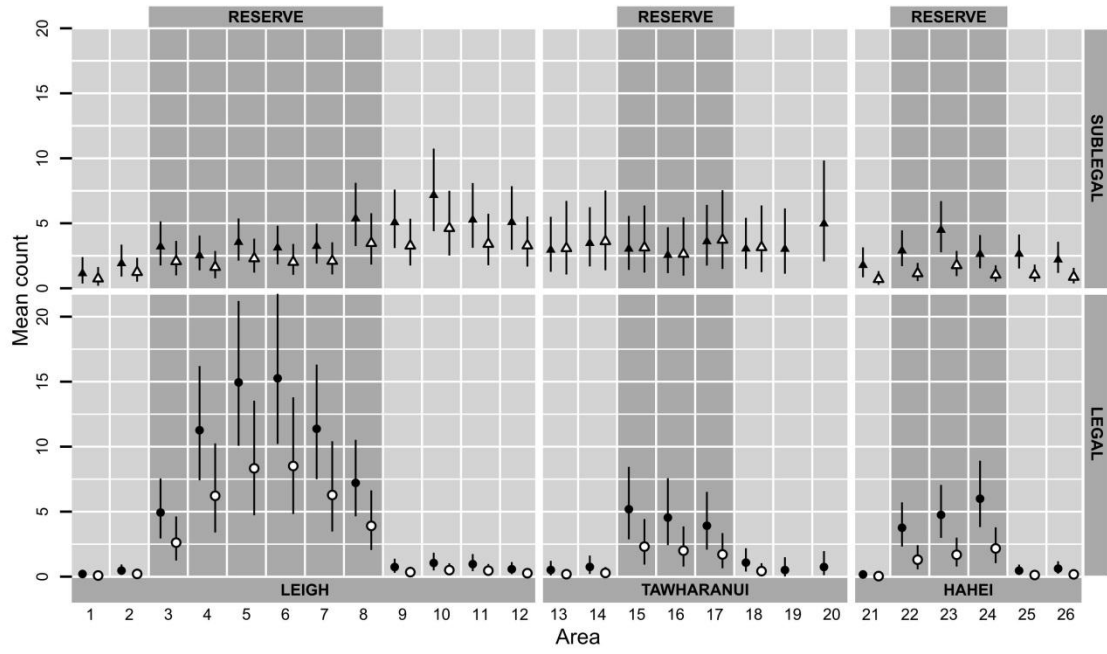


Fig. 3

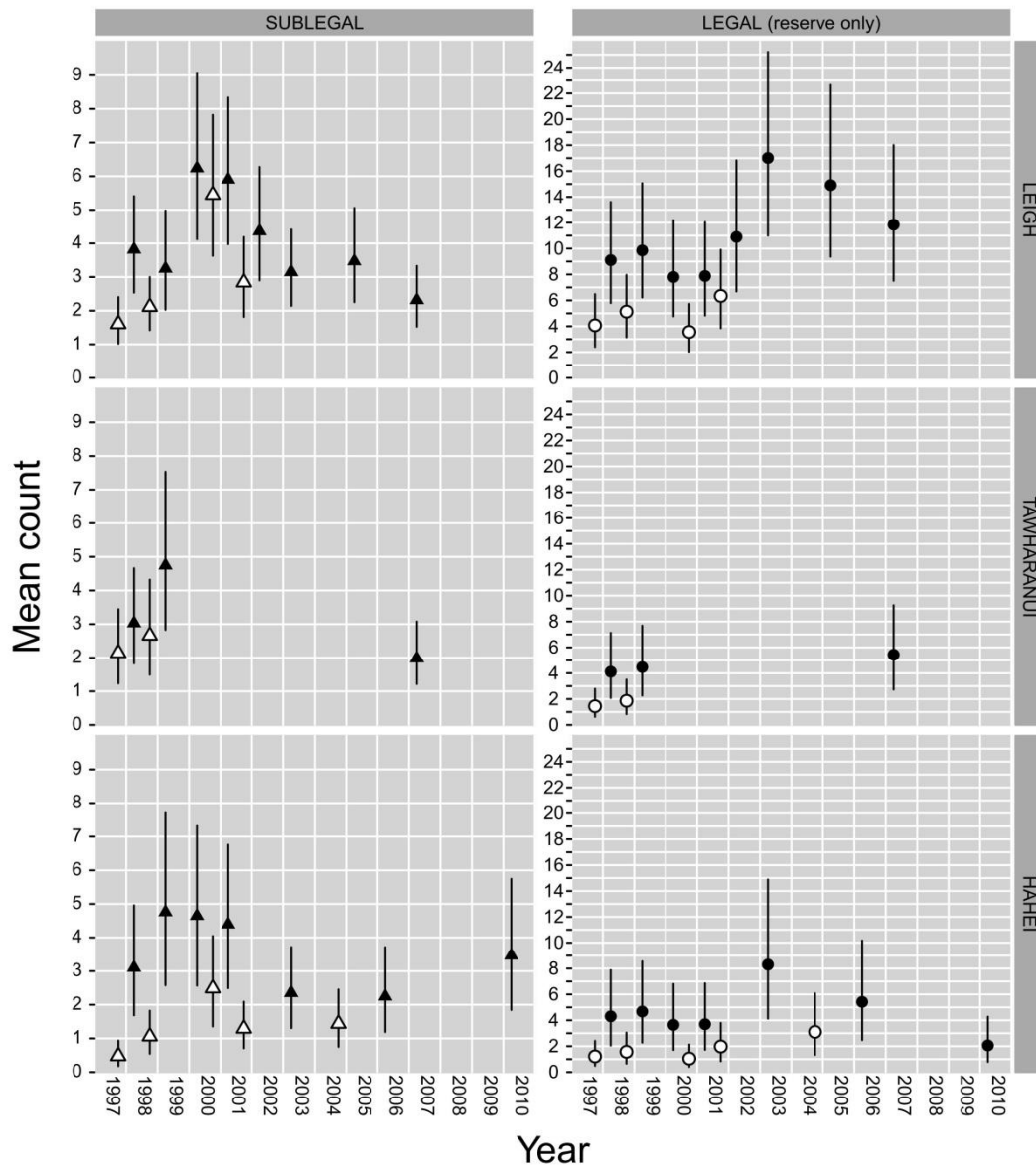


Fig. 4