



Spatial bias in pāua *Haliotis iris* catch-per-unit-effort

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EXECUTIVE SUMMARY

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In fisheries, the exploitation of spatially discrete populations can lead to decoupling of trends in fishery-dependent catch-per-unit-effort (CPUE) and actual stock biomass trends. In this context, abalone (Haliotidae) CPUE is regarded as unreliable in many abalone fisheries worldwide, where stocks are made up of a number of populations with differing biological characteristics.

In New Zealand, however, CPUE still provides the basis for blacklip abalone (pāua; *Haliotis Iris*) stock assessments, despite reliable evidence that management areas contain a mosaic of sub-populations with differing demographic parameters. This assessment approach is of particular concern for pāua management area 7 (PAU 7), in which CPUE has been declining in recent years despite efforts by the fishing industry to rebuild the stock with voluntary reductions in allowable catch.

In this study, a simulation model was developed to investigate how CPUE indices, as estimated from linear models, are influenced by spatial use patterns and by management intervention in the form of reduced catch allowances. Simulations confirmed that spatially-variable resource use, determined by variable productivity in space, can introduce large bias in estimated CPUE indices. I also found predictable bias in the form of hyper-depleted indices after management intervention in the simulated fishery.

Based on this modelling, I then applied a series of increasingly complex spatial and temporal generalised linear mixed models to investigate their ability to mitigate biases arising from spatial use patterns. I found that the most complex space-time model, which explicitly accounted for temporal patterns within small scale populations, can improve bias, especially when it related to the effect of management intervention, but did not necessarily eliminate it.

Applying these models to the CPUE of fishery management area PAU 7, I found that models accounting for temporal dynamics provided the best fit as assessed by model selection criteria; however, they did not confirm the declining trend observed over the most recent years in models that did not explicitly model temporal dynamics in CPUE. Given repeated voluntary reductions in allowable catch in management area PAU 7 over recent years, and the potential for temporally explicit models to reduce such bias, there is a possibility that rebuilding is taking place in this stock, albeit slowly. These new CPUE indices are now being considered as alternative scenarios in stock assessments.

1. INTRODUCTION

Assessing the status of fished populations requires an index of abundance, which is often derived from commercial catch data when no fishery-independent surveys exist. Catch-per-unit-effort (CPUE) is commonly used as a measure that relates capture efficiency to abundance within the conceptually simple model $C = qEB$, where C is catch, E is effort and q is the proportion of biomass, B , removed by a unit of effort. This conceptually simple model, however, belies the considerable bio-economic and socio-ecological complexity that characterises most fisheries. As noted by Hilborn and Walters (1992) “the spatial pattern of abundance, the spatial pattern of fishing effort, and the relationship between abundance and capture success on an individual site all combine to produce the aggregate CPUE.” While CPUE is thus an appealingly simple and cost-effective metric, it is well understood to have a complex relationship with the underlying abundance (Hilborn & Walters 1992, Harley et al. 2001, Maunder et al. 2006).

Some general mechanisms have been studied in the attempt to understand the determinants of the CPUE-abundance relationship (Hilborn & Walters 1992, Maunder et al. 2006). While increased capture success through technological advances and fisher knowledge are clear causes of hyper-stable CPUE (i.e., CPUE declines slower than biomass), spatial patterns in biomass and fishing effort often lead to complex patterns in CPUE (e.g., Prince & Hilborn 1998). The distribution of target species densities, for example, can strongly influence the reliability of CPUE (Clark 1982, Hilborn & Walters 1992, Prince & Hilborn 1998). If the target species is predominantly found in many low-density and few high-density patches,

then fishing down of high-density patches may lead to hyper-depleted CPUE: catch rates decline faster than the actual biomass (because low density patches are not fished; Hilborn & Walters 1992). Similarly, when a fishery contracts into a smaller area (i.e., covers less of the stock area) or reserves are established, CPUE can depict a hyper-depleted picture of the biomass (Walters 2003, Maunder et al. 2006, Ono et al. 2015). Conversely, serial depletion, where a fishery shifts to new areas after areas of high abundance are fished out, will lead to hyper-stable CPUE (Hilborn & Walters 1987, Orensanz et al. 1998, Karpov et al. 2000).

Serial depletion and resulting hyper-stable CPUE indices have been related to a range of fishery collapses (Hilborn & Walters 1992). Abalone (family Haliotidae) stocks, amongst other stocks of sessile invertebrates, are thought to be particularly vulnerable to serial depletion (Prince & Guzmán del Prío 1993, Orensanz et al. 1998, Karpov et al. 2000, Prince 2005). In an example simulation of abalone fisheries, Hilborn and Walters (1987) first showed that the spatial expansion of fishing effort can lead to hyper-stability, and numerous collapses of abalone and other sessile invertebrate fisheries have since been linked to serial depletion (Prince & Guzmán del Prío 1993, Orensanz et al. 1998, Karpov et al. 2000, Kirby 2004). In addition to serial depletion, the aggregating behaviour of abalone makes them prone to over-estimating abundance from CPUE, as abalone densities typically do not decline uniformly over management areas (i.e., their distribution is not ideal free), and it is thought that catch rates remain high and fishing remains economical even at low over-all abundance (Prince 1989).

In abalone fisheries that have operated for a long time (e.g., decades), serial depletion is most likely a relatively minor problem as most reefs will have received repeated fishing effort (Worthington et al. 1998). Nevertheless, the complexities of the fishery may lead to complex relationships between CPUE and abundance. Worthington et al. (1998), for example, demonstrated a non-linear relationship between catch and effort, suggesting that divers achieved higher CPUE at high catches. They attributed this pattern to diver behaviour, with divers working harder (or longer) at high catch rates. Incorporating spatial use patterns may further complicate the relationship of CPUE and abundance in established fisheries, as interactions between diver motivation and spatial resource use can lead to a *de facto* decoupling between CPUE and abundance (Prince & Hilborn 1998).

In New Zealand, CPUE is routinely used as the sole abundance index in the stock assessment of blacklip abalone (*Haliotis iris*; locally known as pāua) (Breen et al. 2003, Fu 2012). Although diver surveys were conducted in a number of management areas over several years, these surveys have been discontinued due to concerns over the methods used (Haist 2010). Although length-frequency data from commercial fishing and limited biological information have been used within the stock assessments, these data are usually only available at a coarse scale, which does not reflect the metapopulation structure of abalone stocks (Prince 2005). In these stock assessments, CPUE has been used as the main variable to date to describe trends in abundance.

Given the importance of CPUE time-series for managing abalone stocks, it is important to consider whether CPUE in New Zealand's pāua fisheries is proportional to biomass. Using newly developed Global Positioning System (GPS) data loggers, fine-scale spatial data were used to calculate catch rates in a fish-down experiment (Abraham & Neubauer 2015). These data suggested that CPUE can be a relatively reliable measure of biomass on small spatial scales, but also showed that spatial resource use even at these small scales leads to non-linear relationships between CPUE and abundance. On larger spatial scales, it is currently unclear how spatial resource use is influencing CPUE. This uncertainty is particularly relevant for quota management area 7 (henceforth PAU 7), where CPUE has remained relatively low, even though the quota has not been fully fished (voluntarily shelved by the industry) in an attempt to recover the stock (recently estimated to be close to 20% of virgin biomass (B_0 ; Fu 2012)). A recent analysis of catch rates from both the high-resolution data loggers and mandatory reporting found a declining trend in CPUE from 2012 to 2015 (Neubauer and Abraham, unpubl. data); this analysis also suggested that a contraction of the fishery over the same period may have artificially lowered the CPUE index.

The present study developed a simulation framework to investigate how CPUE indices, as estimated

in linear models, are influenced by spatial and temporal resource use patterns. It also examined more sophisticated models and definitions of CPUE to establish whether they are robust to these influences, and how estimated CPUE indices for PAU 7 change under alternative model formulations.

2. METHODS

2.1 Simulations

The simulation framework was loosely based on Hilborn and Walters (1987), where spatially discrete populations were exploited by a moving fleet that attempts to maximise catch. Simulations here were designed to gain insight into spatial resource-use dynamics that could lead to bias in pāua CPUE, with a focus on PAU 7.

2.1.1 Stock dynamics

The fishery was divided into a linear coastline of 50 cells (or areas) containing small-scale stocks (indexed with s). Population dynamics within each stock were governed by a delay-difference model (Quinn & Deriso 1999). Given that pāua are sessile (relative to diver movement and fishery spatial scales), individual stocks were considered to be closed, i.e., there was no immigration or emigration at the stock level. Formally,

$$B_{t,s} = (1 + \rho_s)S(B_{t-1,s} - C_{t-1,s}) - \rho_s S^2 \frac{(B_{t-1,s} - C_{t-1,s})}{B_{t-1,s}} (B_{t-2,s} - C_{t-2,s}) + R_{t,s}, \quad (1)$$

$$C_{t-1,s} = \sum_i C_{i,t-1,s} = \sum_i B_{t-1,s} q_i, \quad (2)$$

where B is biomass, C is catch, S is survival, ρ is the Ford growth parameter, R is recruitment and t is taken to be a day. Catchability q was assumed to vary among divers i (although not essential in the following), and the effort was constant each day (i.e., CPUE is catch per day). I did not specifically consider handling time or pāua aggregating behaviour, which leads to predictable decoupling between CPUE and abundance (e.g., Prince 1989), as the present study was focused on spatial-use patterns.

Productivity was stock specific and determined by the growth and recruitment parameters. The Ford growth parameter is defined as $\rho_s = \exp(-\kappa_s)$, with κ_s the von Bertalanffy growth parameter for stock s . The growth parameter varied between stocks s , with parameters for individual stocks drawn from a log-normal distribution, the parameters of which were chosen to approximate values of κ estimated in Helidoniotis et al. (2011). This approach meant that some areas were fast growing, but the majority of areas had medium to slow growth. I further assumed spatial auto-correlation in growth, where $\rho_{s+1} = r\rho_s + (1 - r)\delta_{s+1}$. The parameter δ_{s+1} was a draw from the log-normal distribution, as were $r = 0.5$ and ρ_1 . The parameter $B_{1,s}$ was generated proportional to $p_s = \rho_s \sum_S \rho_s$, in other words, areas with high growth rates also had high initial biomass. I also assumed that areas of fast growth were generally better habitat, and recruitment $R_{t,s}$ was specified to scale with growth, so that areas that produce large-size abalone also have higher recruitment. Additionally, recruitment was specified to be independent of biomass (McShane 1995), and overall production was, therefore, not linked to the spawning stock biomass; fishery management area PAU 7 is usually perceived as a productive stock with strong recruitment (McShane 1997), despite large reductions in biomass inferred from recent assessments. Random fluctuations in recruitment were obtained by multiplying the base recruitment by random numbers drawn from a log-normal distribution for each stock. Natural mortality (and hence survival S) was assumed to be independent of location, with a yearly mortality rate set at $M = 0.15$.

2.1.2 Fisher dynamics

In the simulation, fishers knew the initial status of the biomass in all areas, and also the productivity (which seemed to be a reasonable assumption, see McShane 1997). Their perception of the status of

individual stocks evolved according to Equation 2, but they considered only their own catch (with one exception, see below). Thus, they did not know where other fishers have been fishing, and made decisions about fishing grounds based on their own perception.

Within the simulation, fishers performed a series of stochastic decisions:

1. Whether a fisher decided to go fishing on a given day was determined by a Bernoulli draw, the success probability of which was governed by the maximum expected catch over all areas, relative to the fisher's expectation (taken to be 200 kg day⁻¹). The probability of fishing declined exponentially with declining maximum expected catch.
2. Once the decision to fish was made, fishers chose an area, as a multinomial draw with a probability proportional to the perceived status. The stochastic nature of the decision reflected the stochastic access to sites, as some sites may be optimal, but not fishable at a given day due to weather or other constraints.
3. If the chosen fishing area was already occupied by another fisher, or if the catch in the area (cell) was less than a specified fraction of the expected catch, a move-on rule came into effect. This rule weighed the expected catch in all remaining areas by the distance from the chosen cell, and a new cell was chosen with a weighted probability. The weights were chosen by applying a negative exponential function to the distance from the initially chosen cell.
4. Fishers updated their perception of local biomass by applying their catch, and the catch of fishers they found occupying cells that they chose (but then moved from). In other words, fishers know how much other fishers would remove from a cell, given their perception of the biomass status in that cell.
5. Fishers fished until they reached their quota for a fishing year, which is equally divided among fishers, or until the end of the year.

2.1.3 Simulation runs

Simulation parameters were chosen to reflect the biology of pāua *H. rubra*. Nevertheless, the simulation setup remained somewhat arbitrary, as the spatial grid did not reflect the coastline of fishery management area PAU 7, and is thus not a reflection of the actual population structure. Simulations were built to gain a mechanistic understanding of CPUE reliability in a spatial fishery that is similar to the PAU 7 fishery, and to test standardisation model robustness, rather than to simulate the fishery directly. To this end, I empirically selected ranges of parameters and randomly generated parameters that produced a range of biomass trajectories, rather than aiming to reproduce PAU 7 CPUE trends accurately.

A total of 240 simulations were performed for 20 years each, drawing a random set of parameters for each simulation. The TACC was scaled to productivity so that the biomass declined initially in all simulations over the whole area). After 10 years, the allowable catch was reduced by applying a uniform random multiplier, to allow for varying degrees of recovery. This approach allowed examination of CPUE robustness for both declining and increasing biomass trends, and also of bias introduced by the effect of a management intervention on fisher behaviour.

2.2 CPUE standardisation

Catch was standardised using generalised linear [mixed] models (GL[M]M), applied in a Bayesian context. Models were specified in increasing complexity to account for spatial and temporal patterns in the CPUE data. At the most basic level, the analysis used basic GLMs (model 1) that produced near identical results to a standard generalised linear model analysis of CPUE as currently used for pāua stock assessments. This model was used for exploratory purposes only, and a GLMM was used in all model comparisons, as more complex models built on the random effects formulations. As such a model

is most easily extended in the Bayesian setting, only Bayesian GLMMs were compared. The CPUE GLMM model may be written as

$$\log(C_{i,t,a,s}) \sim N(\mu_{i,t,a,s}, \sigma), \quad (3)$$

$$\mu_{i,t,a,s} = \beta X_{i,t,a,s} + \xi_a + \omega_i + \tau_s, \quad (4)$$

where $C_{i,t,a,s}$ is the catch of diver i at time t in year a and area s ; $N()$ denotes a normal distribution with mean $\mu_{i,t,a,s}$ and standard deviation σ . β is a row vector of regression coefficients; $X_{i,t,a,s}$ is a matrix consisting of an intercept dummy variable and covariates observed for the capture event $C_{i,t,a,s}$; ξ_a is a fixed year effect (usually taken as the CPUE index); the diver effect ω_i and the area effect τ_s were formulated as fixed effects in the GLM (model 1) and as random effects in the GLMM (model 2; glmm). The GLMM was then extended to include spatial and spatio-temporal effects. For the spatial model (model 3; glmm sp), I used a conditional auto-regressive (AR) model to account for spatial auto-correlation of CPUE among adjacent areas/stocks:

$$\tau_s | \tau_{S_s}, \chi \sim N\left(\frac{1}{n_s} \sum_{x \in S_s} \tau_x, \frac{1}{n_s \chi}\right), \quad (5)$$

where S_s is the set of the n_s stocks/cells neighbouring cell s (i.e., all cells other than cell s), and χ is an estimated precision parameter. For the temporal correlation model (model 4; glmm ar), I added a latent auto-regressive process, such that the temporal random effect ν_t is defined as $\nu_t = \rho \nu_{t-1} + \epsilon_t$, where ρ quantifies the spatial auto-correlation and ϵ_t is a normally distributed random increment with estimated standard deviation ϕ , that is $\epsilon_t \sim N(0, \phi)$, thus:

$$\mu_{i,t,a,s} = \beta X_{i,t,a,s} + \xi_a + \omega_i + \eta_{t,s}, \quad (6)$$

and $\eta_{t,s} = \nu_t + \tau_s$ is a realisation of the spatio-temporal random field. (Note that the temporal dynamics are across the whole domain in this case.) Lastly, I explored a slightly more complex model (model 4) that considered $\eta_{s,t}$ with $\nu_{s,t} = \rho \nu_{s,t-1}$, i.e., auto-regressive effects were modelled within each cell.

All models were implemented and estimated in R-INLA (Martins et al. 2013, Rue et al. 2009), an R (R Development Core Team 2008) package for approximate Bayesian inference using integrated nested Laplace approximations for latent Gaussian models (in this case, both latent models, spatial and temporal, are marginally Gaussian)(see Appendix A for model formulation in R-INLA).

2.2.1 CPUE definitions

I tested four different approaches to defining and estimating CPUE. As the base case, I used year effects estimated within the models to define the CPUE index. As time is modelled explicitly at the day scale in temporal models, I also used predicted catch over all areas at three specific times during the fishing year as potential CPUE indices. These times were taken as the last day of the fishing year (EoY index), the last day of the fishery in any year (i.e., the last day at which any of the fishers fished; named the “max index”) and the day when no new areas are fished later in the fishing year (area index).

2.2.2 Exploring sensitivity of CPUE

Three biases were used to explore the sensitivity of CPUE to biomass trends and management intervention. First, the mean bias measures $\frac{1}{A} \sum_{a=1}^A I_{CPUE,a} / I_{B,a}$, where I_{CPUE} and I_B were the CPUE and biomass indices over A years, respectively. The shelving bias was taken to be the bias immediately after the total allowable commercial catch (TACC) was lowered in the simulation. The end bias was the bias at the end of the 20 year time series.

To avoid long fitting times in Bayesian models, I initially fitted a GLM to calculate biases in the index, using Equation 3 with only fixed effects (i.e., diver and area were fixed effects). Biases were then investigated as a function of population and spatial resource use metrics calculated from the simulated data.

I considered a range of metrics, calculated using all years for the mean biases, and the first and last ten years of data for the shelving bias and the end bias, respectively. First, I took the standard deviation of κ within each simulation as a predictor for biases. Second, the biomass slope was taken as the slope of a linear regression of biomass against time. Third, the standard deviation of fishing days was calculated from the number of fishing days in each area within each year. Fourth, the trend in the proportion of biomass subject to fishing was taken as the biomass within all areas fished within a year divided by the total biomass in that year. I then applied a smoother to the data to illustrate patterns in biases due to predictors. Other metrics that were tried but either gave similar trends to metrics outlined above or showed no trend were the trend in proportion of biomass fished, the trend in the inter-quartile range, and the number of areas that were not fished within a day.

Lastly, I used subsets of simulated CPUE indices to investigate if models accounting for spatial and temporal dependencies in the data can decrease biases. I fitted CPUE indices to simulated CPUE data from two subsets of simulation runs, using Bayesian models described in Subsection 2.2. Sub-setting was necessary as the space-time models occasionally took considerable time (several hours) each to fit and extensive memory (over 30 gigabytes) to fit co-variance matrices. The first subset consisted of 40 simulation runs with the highest absolute mean bias. This subset consisted of mainly hyper-depleted indices. To test the performance of more complex CPUE models for less hyper-depleted simulations, I used a second subset of 35 simulations, consisting of the unique subset of the 20 runs with the largest (not absolute) numerical bias for each of the three bias types (i.e., using the least hyper-depleted (or most hyper-stable) indices). Since hyper-depletion dominated indices from simulation runs, the latter subset selected relatively unbiased indices.

2.2.3 Sensitivity to the biological model

To ensure that patterns are related to spatial resource patterns and not the underlying biological model, I repeated the simulations and CPUE model application for simulations using a Schaefer surplus production model instead of the delay-difference model. In the Schaefer model, the intrinsic rate of increase r was taken as the spatially varying productivity parameter, and was drawn from a log-normal distribution as above. The surplus production model was specified as:

$$B_{t,s} = B_{t-1,a} + r_s B_{t-1,s} \left(1 - \frac{B_{t-1,s}}{K_s}\right) - C_{t-1,s} \quad (7)$$

The carrying capacity K_s of stock s was specified to be proportionally greater for productive stocks (i.e., stocks with high r_s). While this model may not be as appropriate for abalone (production is tied to biomass in the preceding time-step), it provides a straightforward way to test whether very different assumptions about stock dynamics lead to similar biases in CPUE.

2.2.4 Applying space-time CPUE models to PAU 7

The CPUE models were applied to CPUE data from PAU 7 since the 2001–02 fishing year, recorded on mandatory reporting forms (pāua catch effort landing returns, PCEL forms). The records include day, effort, diver, dive conditions (using a five category scale) and statistical area, and individual catch information. Effort (log-transformed) and dive condition were taken as predictors in $X_{i,t,a,s}$, whereas diver and statistical area formed the basis of the random effects formulations outlined above.

Models were also fitted to data from the pāua data logger programme, which records spatial effort (i.e., GPS tracks of individual divers) and dive information (depth, time spent diving) at a fine spatial scale. Nevertheless, catch was recorded at a day scale, requiring some assumptions about spatial allocations of catches to apply spatial models. In this case, I took the proportion of time spent diving within each statistical area as a proxy for the catch from that area, and split the catch according to these proportions. Dive metrics were calculated within each statistical area, and included: bottom time (the time that divers

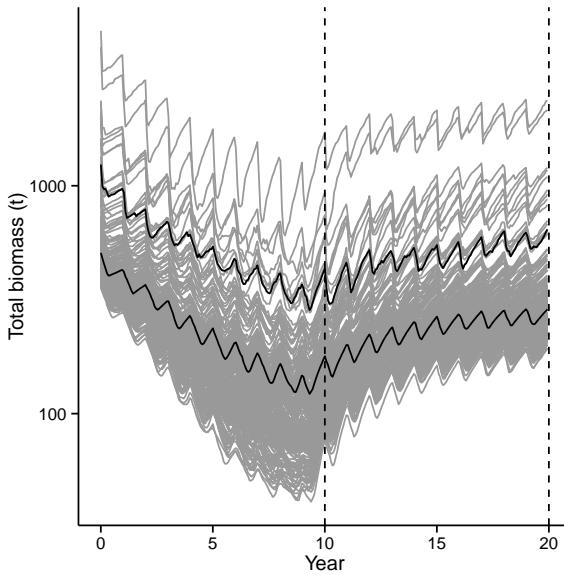


Figure 1: Trends in blacklip abalone (pāua; *Haliotis iris*) biomass over 240 simulations for 20 years each using a delay-difference model. Simulations were used to investigate the potential bias in catch-per-unit-effort introduced by spatial patterns in resource use by abalone fishers in New Zealand management area PAU 7. Black lines show example cases (highlighted in Figure 2 and Figure 3), dashed vertical lines show times at which biases were calculated, including immediately after a reduction in catch (e.g., reduction in quota) at nine years, and at the end of the time series. (Note that biomass was plotted daily, leading to within-year fluctuations.)

spend under water), total fishing time, and median and cumulative depths were taken as possible effort predictors after log-transformation; swell and visibility were included to account for differences in catch due to dive conditions on the day. I then compared indices calculated from the models for the four CPUE metrics.

2.3 Model selection

Model selection was performed using a set of three commonly employed Bayesian model selection metrics. The deviance information criterion (DIC) (Spiegelhalter et al. 2002) is defined as $DIC = -2\log(p(y|\theta)) + pd$, where y is the data, θ is the set of model parameters and pd denotes the effective number of parameters, with the latter term penalising complexity (this measure is similar to the Akaike information criterion in maximum likelihood statistics). The log-score is $LS = E(-\log(p(y_i|y_{-i}, \theta)))$, where E is the expectation, a Bayesian cross-validation measure (Adrian & Mansmann 2012). This measure is less likely to under-penalise complex models, which is a recognised limitation for the DIC in complex hierarchical models. The log marginal likelihood is the log of the probability of the model given the data, $ML = \log(p(M|y))$, where M is the model. The marginal likelihood forms the basis of conventional Bayesian model selection (i.e., the Bayes factor).

3. RESULTS

3.1 Simulations and CPUE bias

Simulations produced a range of behaviours in the total biomass trajectories around the overall trend of declining-shelving-increasing scenario (Figure 1). In general, biomass trajectories that declined further led to larger reductions in catch half-way through the time-series, and fast recovery after the reduction.

Within individual model runs, spatial resource use was strongly driven by the productivity of individual

sites, with the proportion of fishing days in particular areas closely corresponding with relative productivity (Figure 2 a,b). In some simulations, a set of areas were not fished in some years (Figure 2 c); however, in general, all areas in the simulation were fished at some point during the simulation runs. The different levels of shelving produced marked changes in spatial-use patterns. Although they generally reduced the total number of fishing days, they also marked a change from a trend of increasing use of marginal areas during years one through nine (Figure 2 c,d) to a decreasing, then stabilising trend in use of those areas. This outcome was determined by the disproportionate recovery of highly productive areas, which could then account for most of the take.

The standardised catch from the simulations showed strong patterns in bias over time (Figure 3). The majority of indices were hyper-depleted (i.e., bias less than 1), with a tendency to increasing hyper-depletion during the decline, and a further marked increase in bias towards hyper-depletion immediately after the adjustment in allowable catch. After the allowance adjustment, the CPUE indices showed a trend toward stabilisation of the bias, but continued hyper-depletion for the majority of indices (Figure 3).

The overall mean bias was driven by the differences in productivity and the resulting spatial-use patterns (Figure 4 a,b): simulations with large differences in productivity produced more hyper-depleted indices overall (highlighted in Figure 2 for examples of high and low bias). The differences in productivity led to differences in use patterns, namely an increased difference between the number of fishing days in high versus low productivity areas (Figure 4 a,b, Figure 2 c,d). Lower proportions of biomass subjected to fishing each year led to more biased CPUE indices, with an overall trend towards hyper-depletion, but also increasing variability in biases as the proportion of fished biomass decreased (Figure 4 c). The overall biomass trend did not lead to systematic variations of the mean bias (Figure 4 d).

The shelving bias was strongly predicted by changes in the relative frequency of fishing in areas (Figure 4 f). A decrease in the standard deviation of fishing days in different areas was associated with a stronger bias after shelving. The hyper-depletion also increased with increasing biomass trends after shelving (Figure 4 h). There were no marked effects of the growth rate, and the trend in the proportion of biomass fished did not seem strongly related to bias (Figure 4 e,g).

Similar to the mean bias, the end bias was driven by differences in productivity and spatial resource use (Figure 4 i,j), but showed a weaker relationship with the proportion of biomass subjected to fishing (Figure 4 k). At the same time, absolute bias still increased, and became more variable with smaller proportions of biomass subjected to fishing. Simulations with more stable biomass tended to produce less biased estimates (Figure 4 l), but some simulations with large biomass increases also showed relatively small bias.

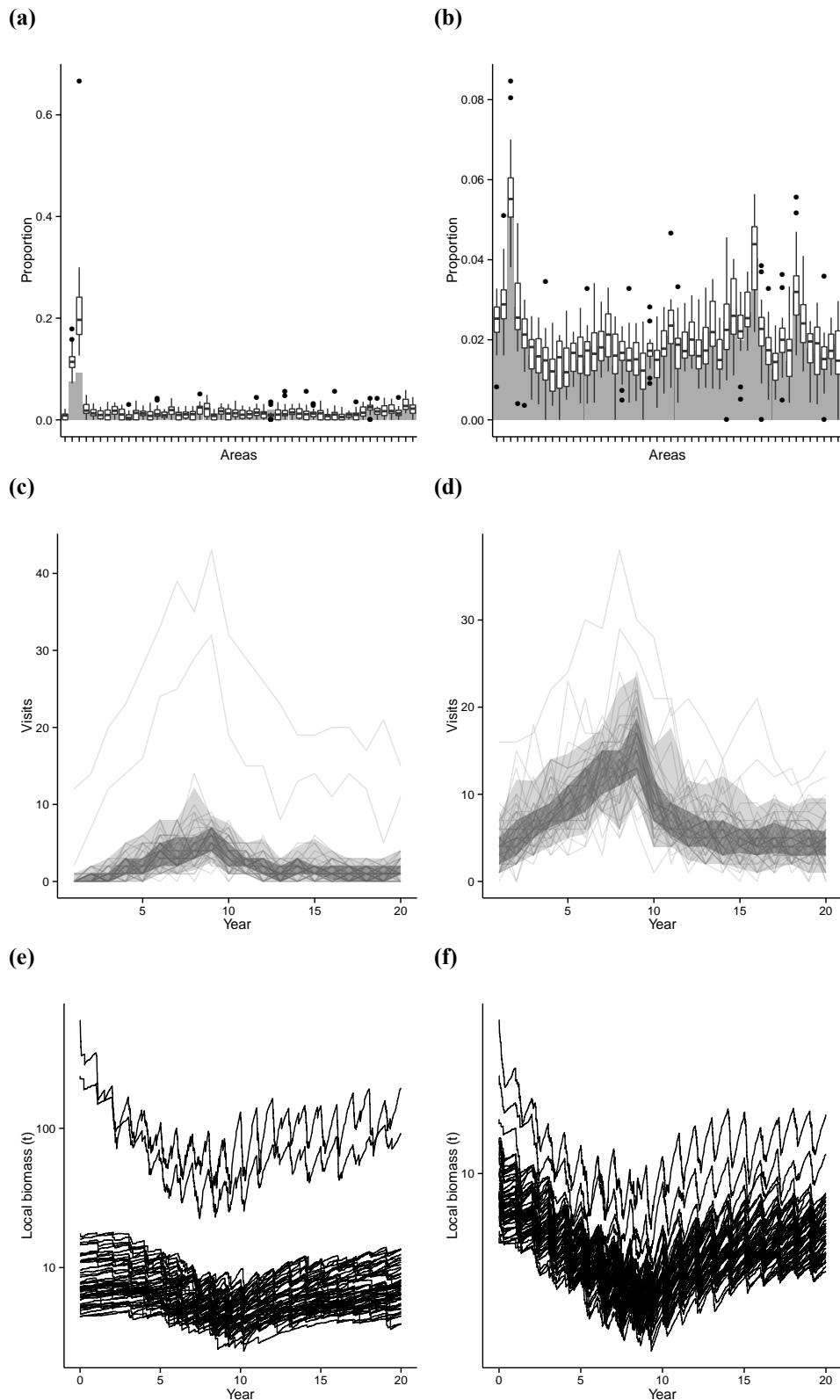


Figure 2: Trends from two individual simulation runs (left and right panels) to investigate the potential bias in catch-per-unit-effort through spatial resource-use dynamics. Simulations were run with high bias (a,c,e) and with relatively low bias (b,d,f). Shown are fishing days (visits) by area over years in the simulated time-series (box-plots) and proportion of total productivity (grey bars; graphs a,b), trends in fishing days by area (c,d; shaded areas indicate 50% and 90% inter-percentile regions), and local biomass trends (e,f; log10 scale for visibility). (Note that biomass is plotted daily, leading to within-year fluctuations.)

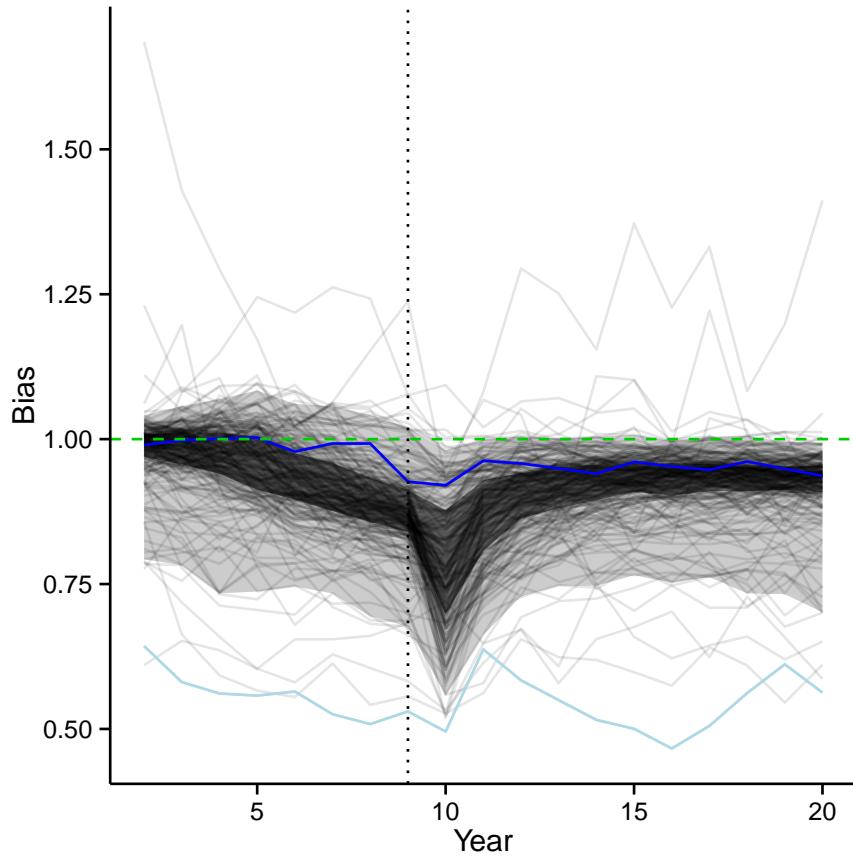


Figure 3: Trend in relative bias of catch-per-unit-effort (CPUE) over the course of individual simulations (grey lines) to investigate the influence of spatial resource-use dynamics on CPUE. The green dashed line indicates the line of no bias, values above and below indicate a hyper-stable and hyper-depleted CPUE index, respectively. Dark shading indicates the inter-quartile range of the bias, lighter shading indicates the 95% range of biases. The light blue line indicates a simulation with high bias (see Figure 2 a,c,e), the dark blue line shows a simulation with relatively low overall bias (see Figure 2 b,d,f). The dotted black line indicates the allowable catch adjustment.

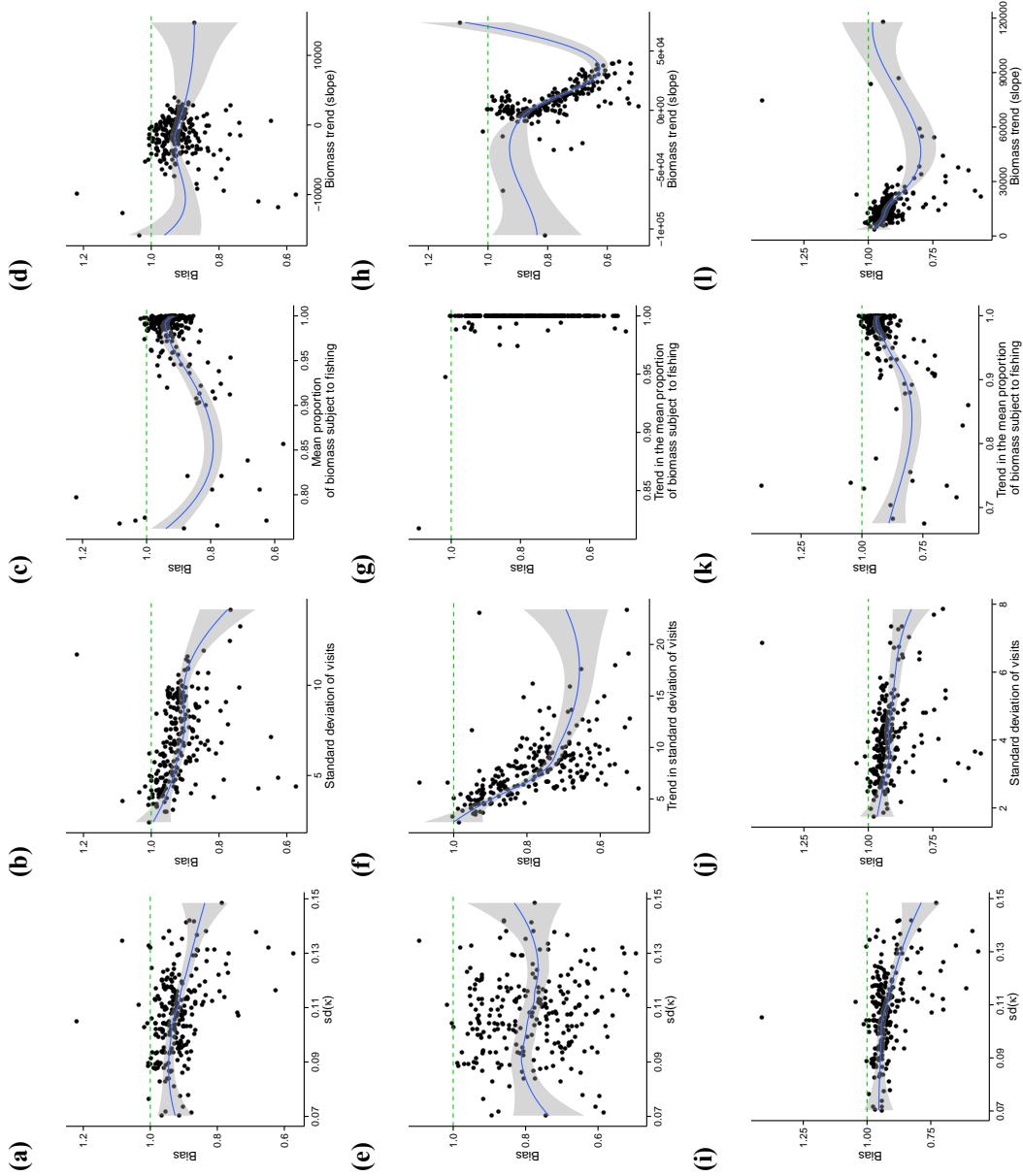


Figure 4: Investigation of bias in catch-per-unit-effort (CPUE) introduced by spatial resource-use dynamics in the blacklip abalone (pāua; *Haliotis iris*) fishery in New Zealand management area PAU 7. Mean bias in CPUE standardisations (a–d), shelving bias (e–h), and end bias (i–l) as a function of the standard deviation of κ (panels a,e,i), the (trend in) standard deviation of yearly fishing days (visits) in areas (b,f,j), the (trend in) proportion of biomass subject to fishing (c,g,k), and the overall biomass trend (kg year^{-1} ; d,h,l). Metrics were calculated for years 1–20 (a–d), years 9–10 (e–h), and years 10–20 (i–l).

Simulations using a surplus production model instead of the delay-difference model also produced biased CPUE indices, but with different trends in biases, and in particular less hyper-depleted indices (Appendix B; Figure B-3). Nevertheless, in this case, large differences in productivity also lead to hyper-depletion (Figure 4). Notably, the bias towards the end of the time series mostly led to over-estimation of rebuilding (Figure B-3).

3.2 CPUE bias with different standardisation models

Comparisons between models applied to both delay-difference model and surplus production model simulations showed an advantage of the spatio-temporal model in addressing biased CPUE time series that result from spatio-temporal complex fishing patterns (Figure 5, Appendix C, Table C-1). For the set of hyper-depleted simulations, the space-time model could not fully eliminate the hyper-depletion in most cases, but it reduced the bias relative to other models for all bias and CPUE index definitions. No CPUE index definition clearly performed better across all bias definitions, but the predictive CPUE index definitions usually led to a larger shelving bias (Table C-1).

For the set of simulations that showed the least hyper-depletion, it was difficult to clearly determine a particular model and CPUE index definition as performing better or worse (Figure C-1, Table C-2). When applied in conjunction with the space-time model, the predictive indices at the last day of fishing (max index) and at the largest extent of the fishery (area index) produced slightly fewer hyper-depleted indices for the mean- and end bias and the mean- and shelf- bias, respectively.

For simulations using the surplus production model (Figure B-1, Figure B-2, Figure B-3, Figure 4), the space-time model produced unbiased estimates of biomass trends for nearly all types of biases and CPUE definitions (Figure C-2, Table C-3). The exceptions to this pattern were two cases of extreme bias throughout. Especially for the end bias, the space-time model provided a considerable improvement over the three other models, which all produced hyper-stable CPUE indices towards the end of the time-series.

3.3 PAU 7 model comparison

Model selection strongly favoured the spatio-temporal models for all model selection metrics (Table 1). A permutation test (using 100 000 permutations) on log-scores obtained from the two best models showed that the probability of observing the difference in mean log-scores (LS) between the two models by chance is only $p = 0.00065$ (Figure 6). There is thus a strong indication that the spatio-temporal model is significantly better than the next best model (temporal auto-regressive, glmm ar). A test against the other two models showed that with 100 000 permutations, the probability was indistinguishable from 0 (i.e., $p < 1e - 05$), suggesting even stronger preference for the spatio-temporal model over these models.

Table 1: Model selection results for three model selection metrics, including the deviance information criterion (DIC), mean log score (ELS), and log marginal likelihood (ML). Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Smaller values indicate better predictive performance of the model.

Model	DIC	ELS	ML
glmm	20879	0.46	-10874
glmm sp	20874	0.46	-10888
glmm ar	19345	0.42	-10221
glmm sp ar	17331	0.38	-9701

The indices for PAU 7, estimated from the different models and CPUE index definitions (Figure 7), showed an increase of nearly 100% between 2001–02 and 2010–11. Nevertheless, after an initial decline between 2010–11 and 2012–13, different models and CPUE definitions suggested different trajectories (see also Appendix D). The standard (base-)index calculated from year effects showed a continued

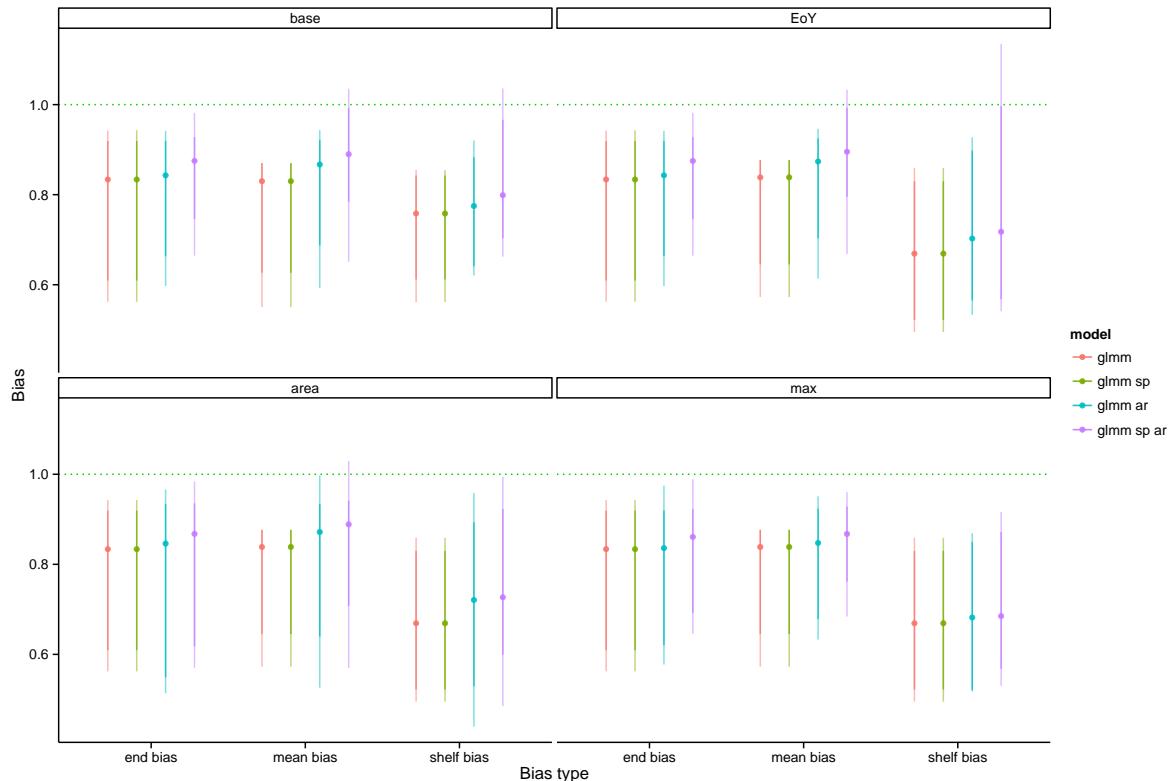


Figure 5: Bias in four catch-per-unit-effort (CPUE) indices estimated from a subset of simulations (40 simulations displaying the largest absolute biases across bias definitions), using a delay-difference model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Plots show the median (dot), inter-quartile-range (IQR; thick line) and the range (thin line) of bias in CPUE indices estimated from four models. Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the end bias (at the end of the time series), the mean bias (average bias over the time series), and the shelf bias (immediately after the simulated quota reduction, i.e., shelving event).

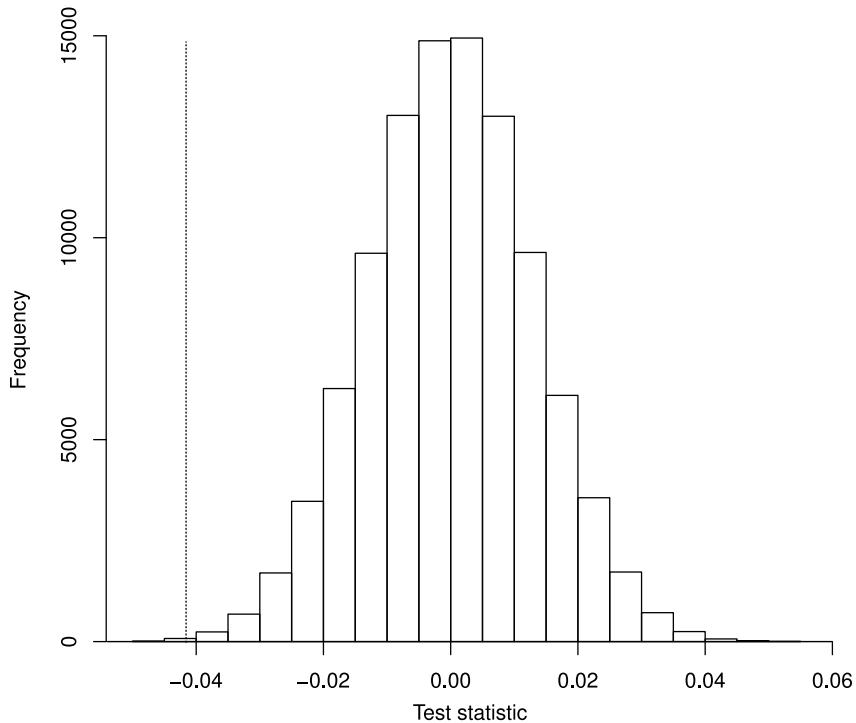


Figure 6: Test statistic $\overline{LS_{M1}} - \overline{LS_{M2}}$ for 100 000 permutations for the spatio-temporal generalised linear mixed model (GLMM, `glmm sp ar`; M1) versus the temporal auto-regressive GLMM (`glmm ar`; M2) used to investigate potential bias in catch-per-unit-effort caused by spatial resource-use dynamics in the blacklip abalone (*pāua; Haliotis iris*) fishery. Vertical line indicates the calculated difference in the test statistic.

decline over the last two fishing years for all models (Figure 7, Table D-3). Similarly, models without temporal dynamics suggested continued declines through the 2014–15 fishing season. Nevertheless, with the area definition of CPUE, both models with temporal dynamics (i.e., the temporal auto-regressive model 4 and spatio-temporal model 5) both showed an upwards trend for the most recent fishing year (Figure 7, Table D-2), and with the max index, both models showed an upward trend for the two most recent fishing years (Figure 7, Table D-1).

The pattern in CPUE indices was similar for CPUE data from loggers (Figure 8, Table D-4). Nevertheless, the space-time model led to the largest decline in the base index from year effects (~15%), relative to other models (~5%). By contrast, the predictive effect from this model over all areas at the last day of the fishery suggested an increasing index, albeit with large uncertainty.

4. DISCUSSION

In this study, I investigated the potential bias in CPUE introduced by spatial patterns in resource use by abalone fishers. The idea that spatial patterns in resource use lead to bias in CPUE is not new, and a number of studies have explored this possibility using simple mathematically tractable models (Clark 1982), simulations (e.g., Hilborn & Walters 1987, Prince 1989, Ono et al. 2015), and conceptual arguments (e.g., Prince & Hilborn 1998). The present study considered this bias in CPUE in the context of depletion and recovery, and sought to investigate biases quantitatively. This investigation included testing how different models of CPUE respond to differing spatial resource use patterns by fishers. Most arguments about bias from spatial resource use concentrate on patch density (Prince 1989, Prince & Hilborn 1998, Dowling et al. 2004a): if abalone increasingly form patches at low biomass levels which divers can easily target, then the CPUE index will be insensitive to changes in biomass and show hyper-stability. In developed fisheries with relatively high exploitation rates, however, this argument is less applicable (Prince 1989). First, individual areas are likely to be re-fished before significant re-aggregation can occur. Second, divers do not fish a single aggregation on a day's fishing, and it is likely that as the density

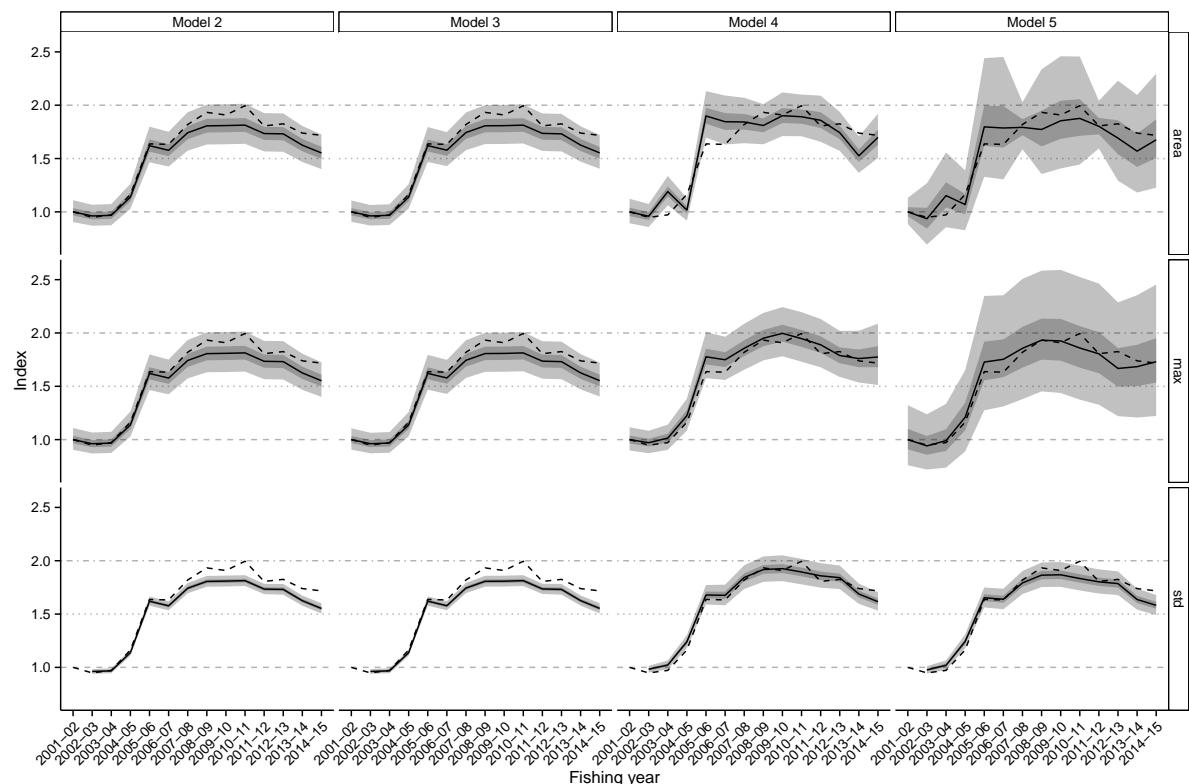


Figure 7: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2001–02 fishing year for blacklip abalone (pāua; *Haliotis iris*) in New Zealand fishery management area PAU 7, obtained from mandatory pāua catch effort landing return forms. Estimates of the posterior mean, inter-quartile range (IQR; dark shading) and 95% confidence interval (light shading) are included for four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. The dashed line shows the raw geometric mean CPUE index.

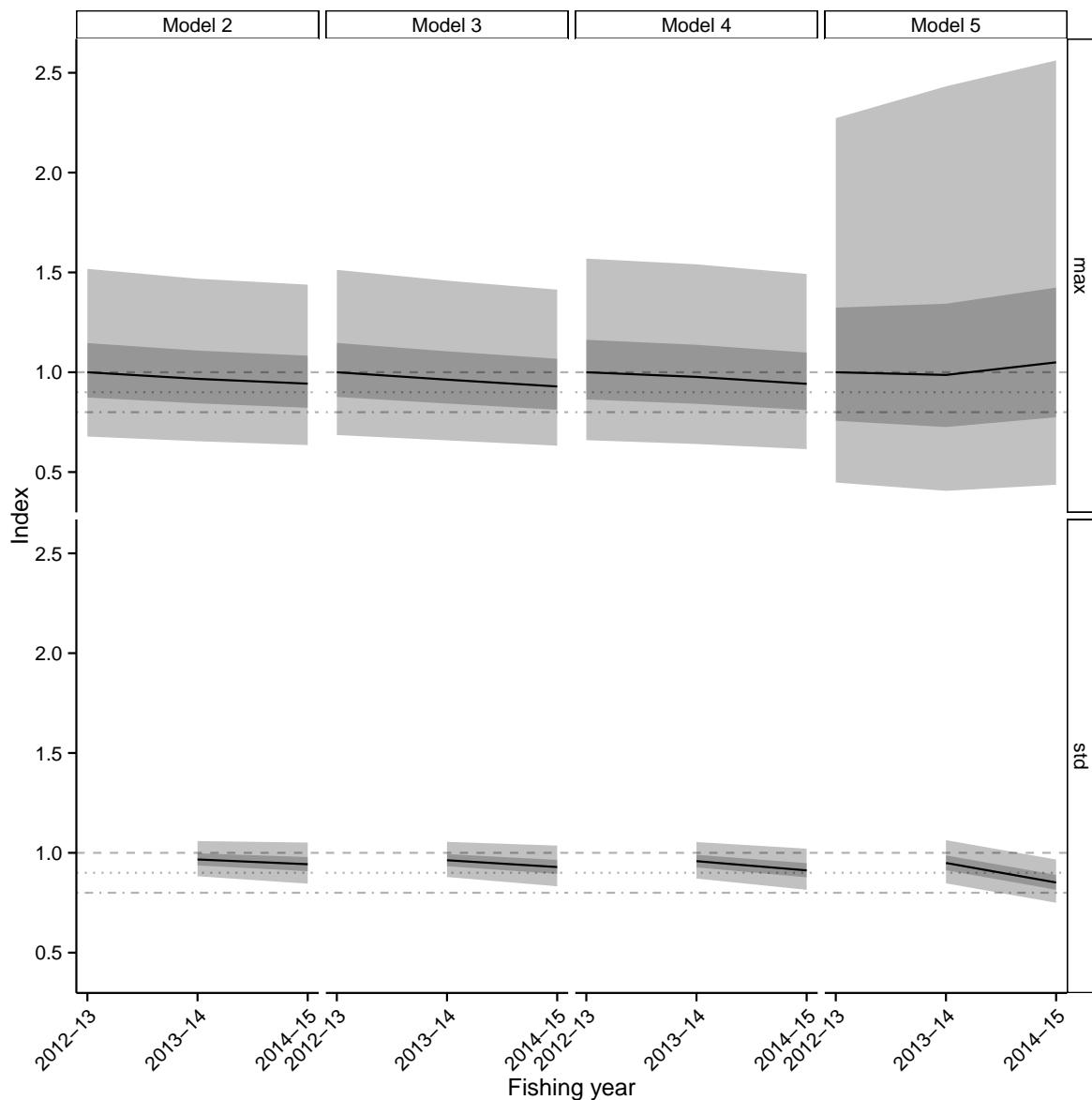


Figure 8: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2012–13 fishing year for blacklip abalone (pāua; *Haliotis iris*) in New Zealand fishery management area PAU 7, obtained from dive data loggers. Estimates of the posterior mean, inter-quartile range (IQR; dark shading) and 95% confidence interval (light shading) are included for four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects.

of high-density patches declines with targeted fishing and declining abundance (Dowling et al. 2004b, McShane 1996), so will daily CPUE. Divers are then more likely to target areas that are productive, and rapidly replenish the exploitable biomass on known abalone beds. These arguments suggest that it is reasonable to assume that CPUE is proportional to biomass at small spatial scales. This assumption is supported by data from a pāua fishdown experiment (Abraham & Neubauer 2015), which suggested that CPUE and abundance were closely related at small scales (but see Dowling et al. 2004a).

Importantly, the simulations demonstrate that despite a possible proportionality between CPUE and abundance at small scales, this proportionality does not readily apply to a larger area comprised of micro-stocks, even in a fishery where most areas are fished each year. In the extreme case, where a large number of areas are not fished, CPUE will considerably underestimate abundance if it does not impute trends in unfished areas (e.g. Walters 2003, Ono et al. 2015). In less extreme cases, where most areas are fished, biases developed via more subtle mechanisms. Investigations of different biases in the simulations suggested that a large difference in the number of fishing days in different areas, determined by their relative productivity, was generally associated with underestimation of relative biomass levels (i.e., a hyper-depleted index) for all biases. The reason for this finding is that productive areas are fished on more days and decline more strongly than areas with fewer fishing days. Thus most of the CPUE will reflect the strong decline in the productive area. This driver clearly predicted the hyper-depletion associated with the shelving event for simulation runs. During the second half of the simulations, at a lower total catch, the reverse happened: as biomass recovered more quickly in the productive areas, simulated fishers moved proportionally more to these areas, especially as a lower catch allowance meant that they needed to fish less to catch their quota.

How relevant are these biases for abalone fisheries, and especially pāua fisheries around New Zealand? There is evidence that stocks in New Zealand are a mosaic of small populations with different demographic rates (McShane et al. 1994, McShane & Naylor 1995, Naylor et al. 2006). Fishing generally targets large aggregations (Dowling et al. 2004b, McShane 1996), and there is some evidence that “hot-spots” of exploitation exist in PAU 7 (Neubauer and Abraham, unpubl. data), and are common in other abalone stocks (e.g., Mundy 2012, Jalali et al. 2015). As such, the model may be representative of general characteristics of pāua and other abalone fisheries.

There was an inevitable degree of arbitrariness in the design of the spatial grid and the distribution of productivity over this grid. For example, estimates of κ (part of the Ford growth parameter) used in the present study were from Tasmanian abalone stocks that may be higher than those of pāua. Nevertheless, the variability in growth is more relevant than the absolute value, and the recruitment part of productivity was arbitrary and scaled to produce simulations that led to reasonable steady state biomass and declines under fishing. Given this arbitrary scaling, resulting biases in real fisheries could be larger or smaller. The surplus production simulations, for example, showed similar patterns of bias for the management intervention (i.e., the reduction in quota), but produced more hyper-stable CPUE indices at the end of the time-series compared with the continued hyper-depletion in the delay-difference case. Relative to the level of bias at the end of the biomass decline (i.e., year 9), however, it was evident that in both cases the spatial resource use lead to overly optimistic inference of recovery, after overly pessimistic assessments of biomass after the reduction in allowable catch.

Furthermore, other factors not considered here, such as handling time, aggregating behaviour, weather- or cost-induced fishing of less desirable regions may move biases in unknown ways. Similarly, biases may be influenced by fluctuations in abundance that are not due to fishing but the results of environmental factors such as sedimentation, disease or warming ocean temperatures (Vilchis et al. 2005). Furthermore, recent dashboards for fishers in individual quota management areas around New Zealand apply some level of data sharing, in which CPUE data at small, statistical area scales are available via an internet-interface and updated throughout the season. Fishers acting on this information may then be more efficient, leading to further distortion of CPUE.

Within the realm of simulated behaviours, tests of increasingly complex standardisation models suggested that the spatio-temporal model was able to, on average, improve (for the delay-difference model) or

eliminate (for the surplus production case) bias. This model was relatively complex compared with most classic CPUE standardisation approaches (Venables & Dichmont 2004, Maunder & Punt 2004), but this complexity was necessary to improve modelling of trends at the level of individual areas. It furthermore extends a line of recent research suggesting that spatio-temporal models can yield improvements in accuracy of abundance indices (Thorson & Ward 2013) and produce more biologically plausible and interpretable trends (Shelton et al. 2014). Given the apparent reduction in bias from spatial resource use in simulations, an application of this model or a similar form should be considered for standardisation of commercial catch rates in New Zealand fisheries.

The current finding of different levels of bias among different definitions of CPUE for the space-time model suggested that the performance of the indices is context-dependent. Most often, a CPUE index is constructed by estimating the year coefficients (i.e., ξ) relative to a reference year (Maunder & Punt 2004). Nevertheless, when the spatial distribution of fishing and the fished resource are uneven, the intensity of exploitation and the chronology of exploitation will affect CPUE. For example, if two fishing crews choose to fish the same reef within days of each other, the second crew will have a lower CPUE that reflects the harvest of the first crew. If that second crew, however, fished months later within the same fishing year, they might obtain the same or higher CPUE (depending on in-season growth), thus inflating the mean CPUE. Since the year effect models mean CPUE regardless of the fishing pattern, it does not have a clear link to biomass. In the above example, CPUE corresponds neither with the biomass available to either crew one or two. Similarly, if fishers concentrate on one productive reef, and fish a less productive area only late in the season, CPUE will represent a mean CPUE over the whole season for the productive area, but only reflect biomass late in the year at the less productive spot, meaning that the CPUE index does not refer to the same biological quantity at the two different reefs. In the extreme, when fishers do not fish a particular area in a given year, then CPUE does not account for trends in that area at all (Ono et al. 2015). In this sense, the predictive indices are more easily interpreted: they are estimates of what catches (or catch rates) would have been at a particular time of year under standard conditions (see also Walters 2003). Yet, as they integrate over uncertainty in local trends, they also have inherently higher uncertainty. But given the small-scale variability of abalone demographics, this uncertainty may be more representative of the true uncertainty in relative abundance trends than the low uncertainty around estimated year effects in standard GLM standardisation models.

The application of the space-time model to fishery management area PAU 7 produced similar estimates of mean indices, except for the predictive end-of-fishing-year index. This predictive CPUE index performed worse than other indices in terms of shelving-bias from the standardisations of simulated data, but did slightly reduce the shelving bias and was unbiased overall. Thus, it may be taken as an alternative scenario, especially since PAU 7 has undergone repeated shelving of increasing proportions of the TACC.

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A. INLA CPUE STANDARDISATION MODELS

The following gives the R-INLA models used to standardise catch-per-unit-effort (CPUE) in simulations (statistical areas in formulae are synonymous with cells in that case) and in quota management area PAU 7. Note that catch here is the log catch, effort is the daily effort (not used in simulated fishing as all effort was equal among days). The SA.graph is the neighbour graph of statistical areas in PAU 7.

```
glm_model <- catch ~ fishing_year + condition + effort + factor(diver) +
  factor(Statistical.Area)

glmm_model <- catch ~ fishing_year + condition + effort +
  f(Statistical.Area,model='iid') +
  f(diver,model='iid')

glmm_sp_model <- catch ~ fishing_year + condition + effort +
  f(Statistical.Area,model='besag',graph='SA.graph') +
  f(diver,model='iid')

glmm_ar_model <- catch ~ fishing_year + condition + effort +
  f(Statistical.Area,model='besag',graph='SA.graph') +
  f(diver,model='iid')+
  f(day,model='ar1')

glmm_sp_ar_model <- catch ~ fishing_year + condition + effort +
  f(Statistical.Area,model='besag',graph='SA.graph') +
  f(diver,model='iid')+
  f(day,model='ar1',group=Statistical.Area,control.group = list(model="exchangeable"))
```

B. SPATIAL RESOURCE USE IN SIMULATION RUNS WITH THE SURPLUS PRODUCTION MODEL

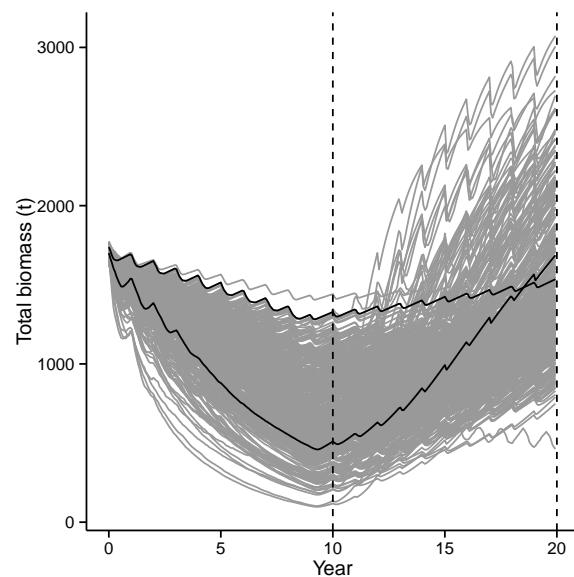


Figure B-1: Trends in blacklip abalone (pāua; *Haliotis iris*) biomass over 240 simulations for 20 years each using a spatial surplus production model. Black lines show example cases (highlighted in Figure 2), dashed vertical lines show times at which biases were calculated, including immediately after a reduction in catch (e.g., reduction in quota) at nine years, and at the end of the time series. (Note that biomass was plotted daily, leading to within-year fluctuations.)

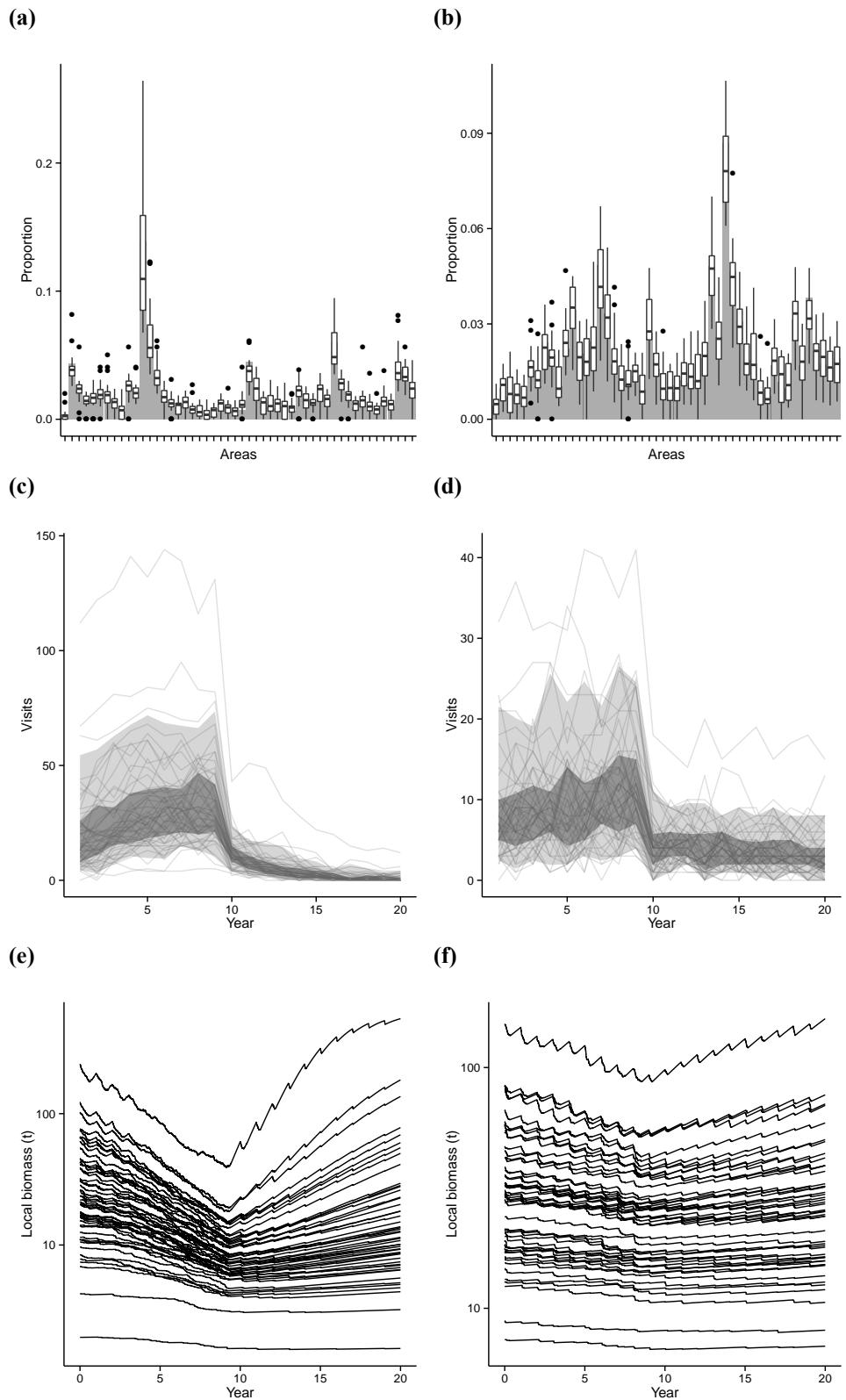


Figure B-2: Trends from two individual simulation runs (left and right panels) using a surplus production model. Shown are fishing days by area over years in the simulated time-series (box plots) and proportion of total productivity (grey bars; graphs a,b), trends in visits by area (graphs c,d; shaded areas are the 50% and 90% interpercentile regions), and local biomass trends (graphs e,f; log10 scale for visibility). (Note that biomass is plotted daily, leading to within-year fluctuations.)

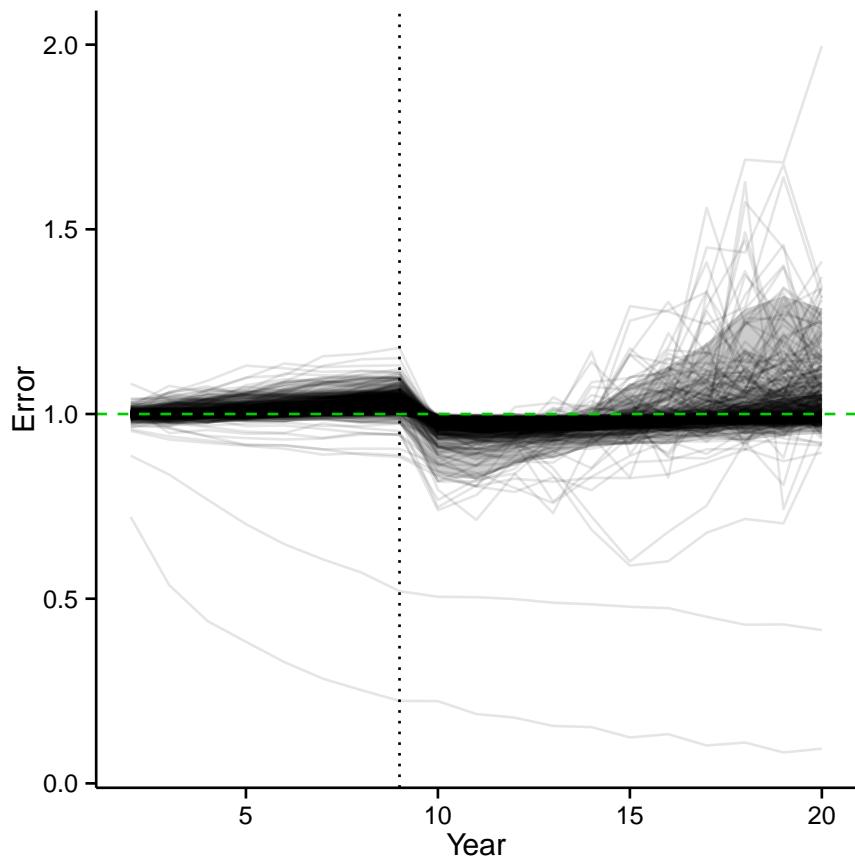


Figure B-3: Trend in relative bias of catch-per-unit-effort (CPUE) over the course of individual simulations (grey lines) to investigate the influence of spatial resource-use dynamics and management on CPUE using a spatial surplus production model. Green dashed line indicates line of no bias, values above and below line indicate a hyper-stable and hyper-depleted index, respectively. Dark shading indicates the interquartile range of the biases, lighter shading indicates the 95% range of bias. Dotted black line indicates the allowable catch adjustment.

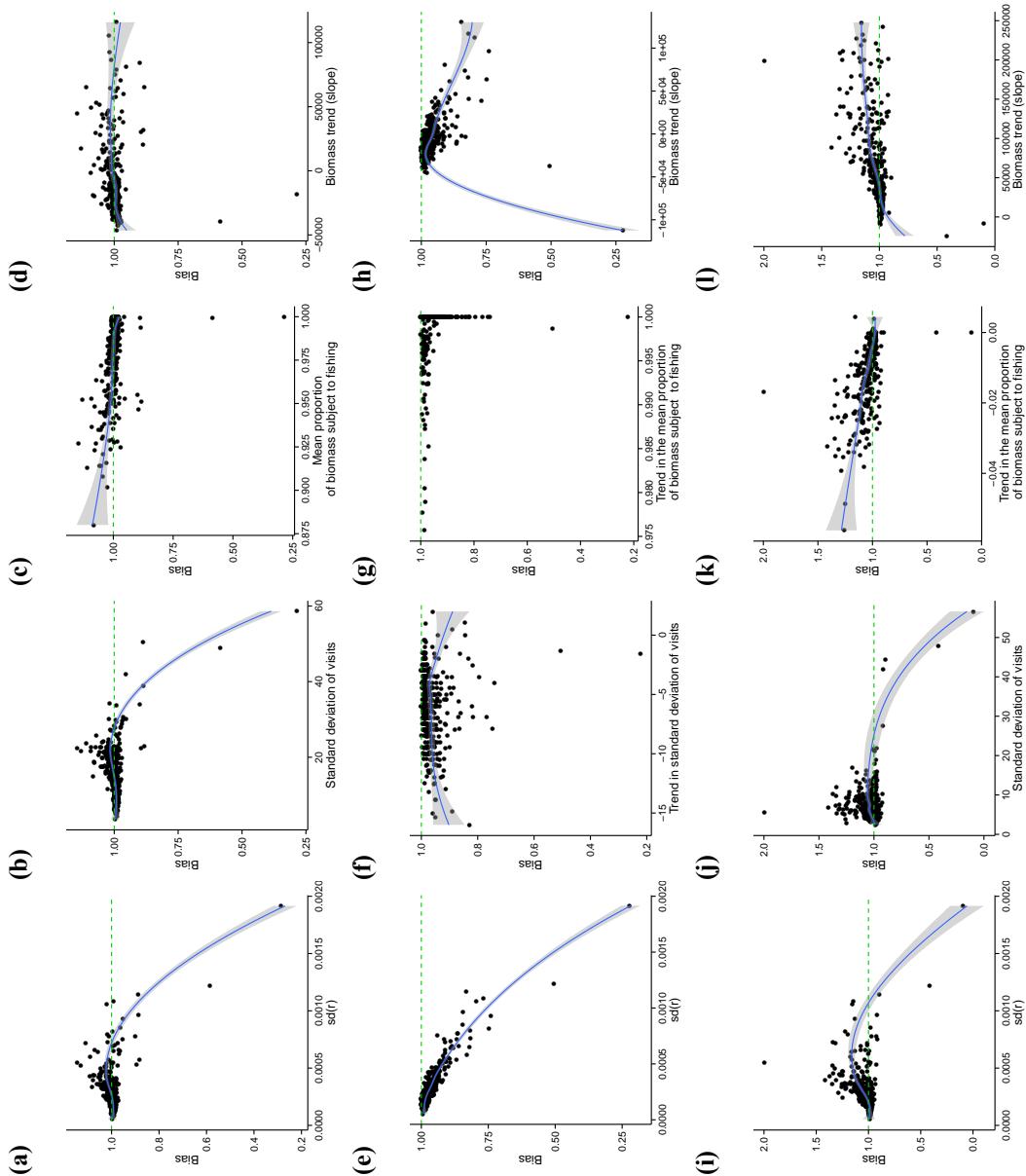


Figure B-4: Investigation of bias in catch-per-unit-effort (CPUE) introduced by spatial resource-use dynamics using a spatial surplus production model. Mean bias in CPUE standardisations (a–d), shelving bias (e–h), and end bias (i–l) as a function of the standard deviation of κ (panels a,e,i), the (trend in) standard deviation of yearly fishing days (visits) in areas (b,f,j), the (trend in) proportion of biomass subject to fishing (c,g,k), and the overall biomass trend (kg year $^{-1}$; d,h,l). Metrics were calculated for years 1–20 (a–d), years 9–10 (e–h), and years 10–20 (i–l).

C. SIMULATION BIAS COMPARISON

Table C-1: Bias in four catch-per-unit-effort (CPUE, estimates of the mean and standard deviation) indices estimated from a subset of simulations (40 simulations displaying the largest absolute biases across bias definitions), using a delay-difference model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the mean bias (average bias over the time-series), the shelving bias (immediately after the simulated quota reduction, i.e., shelving event), and the end bias (at the end of the time series).

Type	Model	mean bias		shelve bias		end bias	
		Mean	sd	Mean	sd	Mean	sd
base	glmm	0.80	0.08	0.74	0.07	0.81	0.10
	glmm sp	0.80	0.08	0.74	0.07	0.81	0.10
	glmm ar	0.85	0.07	0.78	0.08	0.82	0.08
	glmm sp ar	0.89	0.07	0.82	0.09	0.85	0.07
area	glmm	0.81	0.07	0.67	0.10	0.81	0.10
	glmm sp	0.81	0.07	0.67	0.10	0.81	0.10
	glmm ar	0.84	0.10	0.71	0.11	0.81	0.12
	glmm sp ar	0.87	0.08	0.74	0.11	0.83	0.10
max	glmm	0.81	0.07	0.67	0.10	0.81	0.10
	glmm sp	0.81	0.07	0.67	0.10	0.81	0.10
	glmm ar	0.83	0.08	0.67	0.10	0.81	0.10
	glmm sp ar	0.86	0.06	0.70	0.10	0.83	0.08
EoY	glmm	0.81	0.07	0.67	0.10	0.81	0.10
	glmm sp	0.81	0.07	0.67	0.10	0.81	0.10
	glmm ar	0.86	0.07	0.72	0.11	0.82	0.08
	glmm sp ar	0.89	0.06	0.76	0.14	0.85	0.07

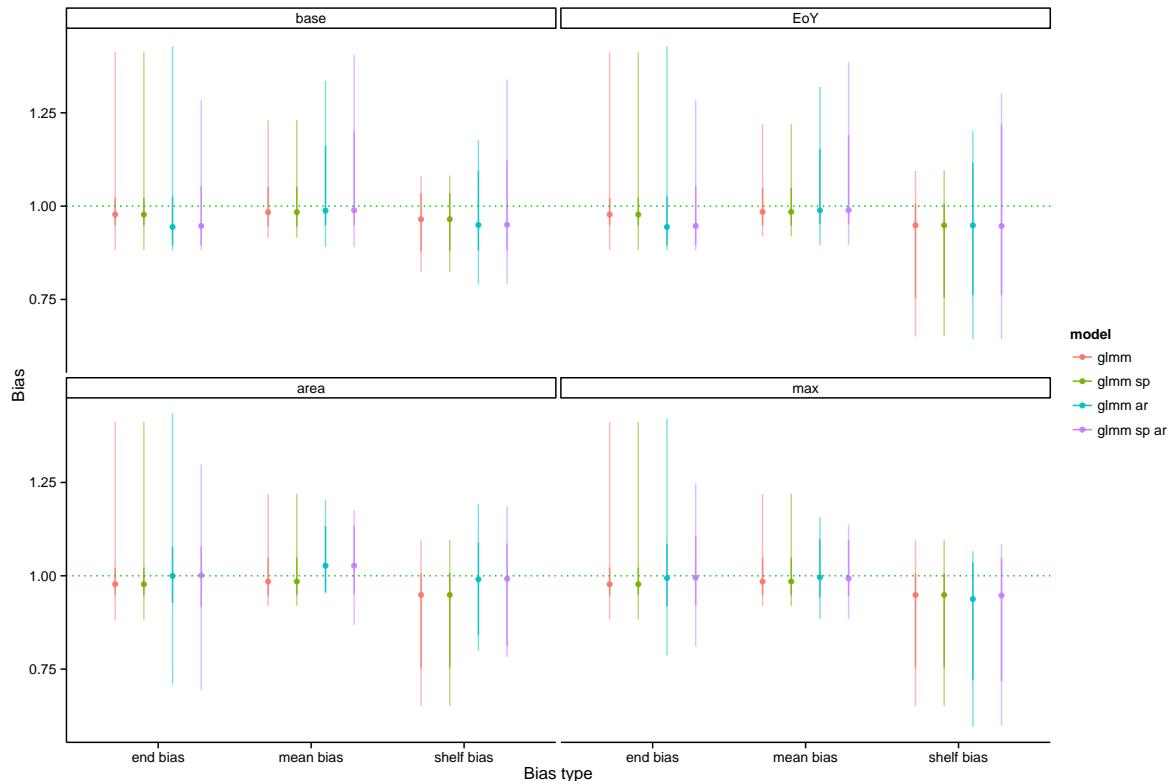


Figure C-1: Bias in four catch-per-unit-effort (CPUE) indices estimated from a subset of simulations (40 simulations displaying the largest absolute biases across bias definitions), using a delay-difference model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Plots show the median (dot), interquartile-range (IQR; thick line) and the range (thin line) of bias in CPUE indices estimated from four models. Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the end bias (at the end of the time series), the mean bias (average bias over the time series), and the shelving bias (immediately after the simulated quota reduction, i.e., shelving event).

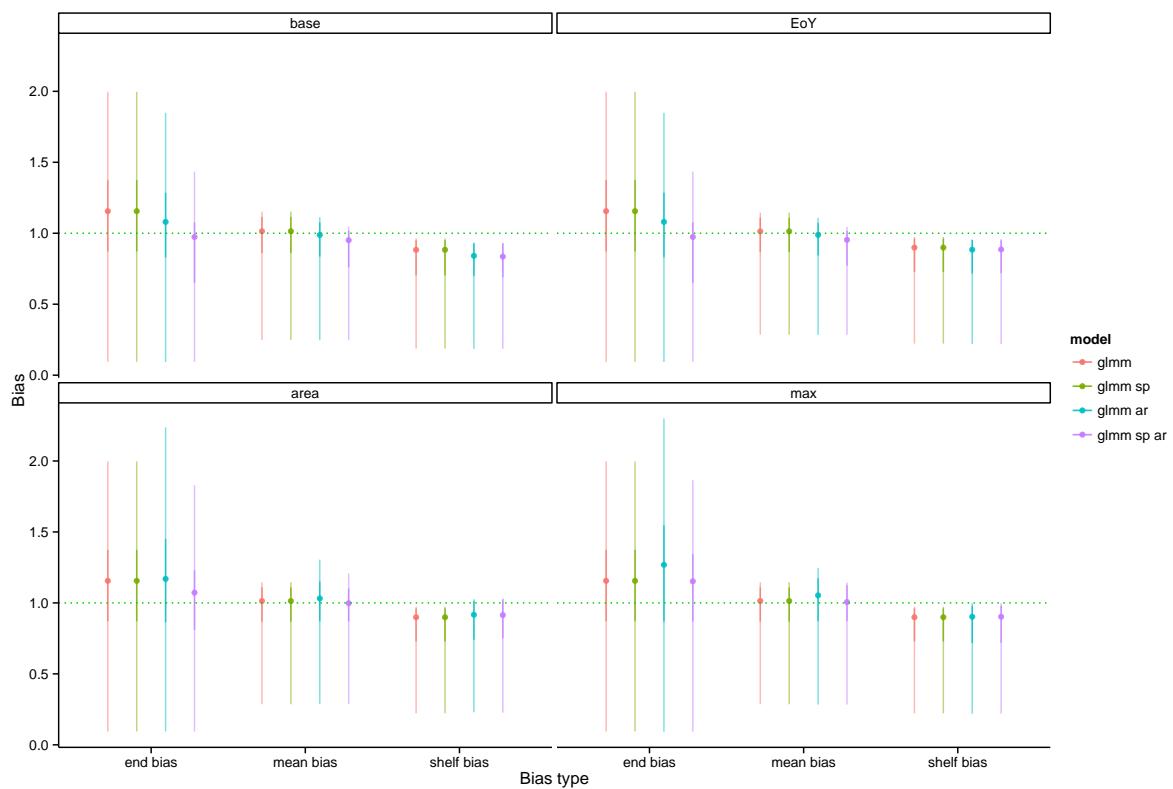


Figure C-2: Bias in four catch-per-unit-effort (CPUE) indices estimated from a subset of simulations (40 simulations displaying the highest absolute biases) using a surplus production model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Plots show the median (dot), interquartile range (IQR; thick line) and the range (thin line) of bias in CPUE indices estimated from four models. Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the end bias (at the end of the time series), the mean bias (average bias over the time series), and the shelving bias (immediately after the simulated quota reduction, i.e., shelving event).

Table C-2: Bias in four catch-per-unit-effort (CPUE, estimates of the mean and standard deviation) indices estimated from a subset of simulations (35 simulations displaying the least hyper-depletion across bias definitions), using a delay-difference model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the mean bias (average bias over the time-series), the shelf bias (immediately after the simulated quota reduction, i.e., shelving event), and the end bias (at the end of the time series).

Type	Model	mean bias		shelf bias		end bias	
		Mean	sd	Mean	sd	Mean	sd
base	glmm	0.99	0.05	0.96	0.05	0.99	0.08
	glmm sp	0.99	0.05	0.96	0.05	0.99	0.08
	glmm ar	1.01	0.08	0.96	0.07	0.96	0.09
	glmm sp ar	1.01	0.09	0.96	0.09	0.96	0.07
area	glmm	0.99	0.05	0.93	0.08	0.99	0.08
	glmm sp	0.99	0.05	0.93	0.08	0.99	0.08
	glmm ar	1.04	0.06	1.00	0.08	1.01	0.10
	glmm sp ar	1.04	0.06	1.00	0.08	1.00	0.09
max	glmm	0.99	0.05	0.93	0.08	0.99	0.08
	glmm sp	0.99	0.05	0.93	0.08	0.99	0.08
	glmm ar	1.00	0.05	0.92	0.10	1.00	0.09
	glmm sp ar	1.00	0.05	0.92	0.10	1.00	0.07
EoY	glmm	0.99	0.05	0.93	0.08	0.99	0.08
	glmm sp	0.99	0.05	0.93	0.08	0.99	0.08
	glmm ar	1.01	0.07	0.94	0.10	0.96	0.09
	glmm sp ar	1.01	0.09	0.95	0.13	0.96	0.07

Table C-3: Bias in four catch-per-unit-effort (CPUE, estimates of the mean and standard deviation) indices estimated from a subset of simulations (40 simulations displaying the highest absolute biases) using a surplus production model for blacklip abalone (pāua; *Haliotis iris*) stock dynamics. CPUE indices were estimated from the year effects (base index), or predictions at the maximum spatial extent of the fishery in a fishing year (area index), the last fishing day of each fishing year (max index) and the last day of the fishing year (EoY index; the day before the new season). Models were a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects. Biases included the mean bias (average bias over the time series), the shelving bias (immediately after the simulated quota reduction, i.e., shelving event), and the end bias (at the end of the time series).

Type	Model	mean bias		shelf bias		end bias	
		Mean	sd	Mean	sd	Mean	sd
base	glmm	0.98	0.15	0.85	0.13	1.12	0.29
	glmm sp	0.98	0.15	0.85	0.13	1.12	0.29
	glmm ar	0.96	0.15	0.82	0.13	1.06	0.26
	glmm sp ar	0.92	0.14	0.82	0.13	0.93	0.20
area	glmm	0.98	0.15	0.86	0.13	1.12	0.29
	glmm sp	0.98	0.15	0.86	0.13	1.12	0.29
	glmm ar	1.01	0.16	0.88	0.14	1.15	0.32
	glmm sp ar	0.97	0.14	0.88	0.14	1.04	0.25
max	glmm	0.98	0.15	0.86	0.13	1.12	0.29
	glmm sp	0.98	0.15	0.86	0.13	1.12	0.29
	glmm ar	1.02	0.16	0.87	0.14	1.23	0.34
	glmm sp ar	0.98	0.15	0.87	0.14	1.10	0.27
EoY	glmm	0.98	0.15	0.86	0.13	1.12	0.29
	glmm sp	0.98	0.15	0.86	0.13	1.12	0.29
	glmm ar	0.96	0.14	0.84	0.13	1.06	0.26
	glmm sp ar	0.92	0.13	0.84	0.13	0.93	0.20

D. PAU 7 MODEL COMPARISON

Table D-1: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2001–02 fishing year for blacklip abalone (pāua; *Haliotis iris*) in New Zealand quota management area PAU 7, obtained from mandatory pāua catch effort landing return forms. CPUE indices were estimated from predictions at the last fishing day of each fishing year (max index), and include the posterior mean, interquartile range (IQR) and 95% confidence interval (CI) for each of four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects.

Index type	Fishing year	glmm			glmm sp			glmm ar			glmm sp ar		
		Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI
max	2002-03	0.96	0.93-1	0.87-1.07	0.96	0.93-1	0.87-1.06	0.97	0.94-1.01	0.87-1.08	0.94	0.86-1.03	0.72-1.24
	2003-04	0.97	0.93-1	0.87-1.07	0.97	0.94-1	0.88-1.07	1.01	0.97-1.06	0.9-1.14	0.99	0.89-1.1	0.74-1.34
	2004-05	1.14	1.1-1.18	1.03-1.26	1.14	1.1-1.18	1.03-1.26	1.22	1.17-1.28	1.09-1.38	1.21	1.09-1.35	0.89-1.65
	2005-06	1.62	1.56-1.68	1.46-1.8	1.62	1.57-1.68	1.47-1.8	1.78	1.7-1.85	1.58-2.01	1.73	1.56-1.92	1.28-2.35
	2006-07	1.58	1.52-1.63	1.43-1.75	1.58	1.52-1.63	1.43-1.75	1.75	1.68-1.82	1.56-1.96	1.75	1.59-1.94	1.31-2.35
	2007-08	1.74	1.68-1.81	1.57-1.93	1.74	1.68-1.81	1.58-1.93	1.86	1.78-1.93	1.66-2.09	1.86	1.68-2.06	1.38-2.51
	2008-09	1.81	1.74-1.87	1.63-2.01	1.81	1.75-1.87	1.64-2	1.95	1.88-2.03	1.74-2.19	1.93	1.75-2.13	1.45-2.58
	2009-10	1.81	1.75-1.87	1.63-2.01	1.81	1.75-1.87	1.64-2	2.00	1.92-2.08	1.78-2.24	1.93	1.74-2.13	1.44-2.59
	2010-11	1.81	1.75-1.88	1.64-2.01	1.81	1.75-1.88	1.64-2.01	1.95	1.87-2.03	1.73-2.2	1.86	1.67-2.06	1.37-2.52
	2011-12	1.73	1.67-1.8	1.57-1.93	1.74	1.68-1.8	1.57-1.92	1.89	1.81-1.97	1.68-2.13	1.80	1.62-2.01	1.33-2.46
	2012-13	1.73	1.67-1.79	1.56-1.92	1.73	1.67-1.79	1.57-1.92	1.79	1.72-1.86	1.59-2.02	1.67	1.5-1.86	1.22-2.29
	2013-14	1.63	1.57-1.68	1.47-1.81	1.63	1.57-1.68	1.47-1.8	1.76	1.68-1.85	1.54-2.02	1.68	1.5-1.89	1.21-2.35
	2014-15	1.55	1.5-1.61	1.4-1.73	1.55	1.5-1.61	1.4-1.72	1.77	1.68-1.88	1.51-2.09	1.73	1.54-1.95	1.22-2.45

Table D-2: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2001–02 fishing year for blacklip abalone (pāua; *Haliotis iris*) in New Zealand quota management area PAU 7, obtained from mandatory pāua catch effort landing return forms. CPUE indices were estimated from predictions at the maximum spatial extent of the fishery in a fishing year (area index), and include the posterior mean, interquartile range (IQR) and 95% confidence interval (CI) for each of four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects.

Index type	Fishing year	glmm			glmm sp			glmm ar			glmm sp ar		
		Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI
area	2002-03	0.96	0.93-1	0.87-1.07	0.96	0.93-1	0.87-1.06	0.96	0.92-1	0.86-1.07	0.94	0.84-1.04	0.69-1.27
	2003-04	0.97	0.93-1	0.87-1.07	0.97	0.94-1	0.88-1.07	1.19	1.14-1.24	1.06-1.34	1.15	1.04-1.28	0.86-1.56
	2004-05	1.14	1.1-1.18	1.03-1.26	1.14	1.1-1.18	1.03-1.26	1.02	0.98-1.05	0.92-1.13	1.07	0.98-1.17	0.83-1.39
	2005-06	1.62	1.56-1.68	1.46-1.8	1.62	1.57-1.68	1.47-1.8	1.90	1.83-1.98	1.7-2.13	1.80	1.62-2	1.33-2.44
	2006-07	1.58	1.52-1.63	1.43-1.75	1.58	1.52-1.63	1.43-1.75	1.85	1.77-1.93	1.63-2.09	1.79	1.6-1.99	1.3-2.45
	2007-08	1.74	1.68-1.81	1.57-1.93	1.74	1.68-1.81	1.58-1.93	1.84	1.77-1.92	1.64-2.07	1.79	1.72-1.87	1.59-2.03
	2008-09	1.81	1.74-1.87	1.63-2.01	1.81	1.75-1.87	1.64-2	1.81	1.75-1.88	1.63-2.01	1.77	1.61-1.95	1.35-2.34
	2009-10	1.81	1.75-1.87	1.63-2.01	1.81	1.75-1.87	1.64-2	1.90	1.83-1.97	1.71-2.12	1.85	1.68-2.04	1.41-2.46
	2010-11	1.81	1.75-1.88	1.64-2.01	1.81	1.75-1.88	1.64-2.01	1.89	1.83-1.96	1.71-2.1	1.88	1.71-2.06	1.44-2.46
	2011-12	1.73	1.67-1.8	1.57-1.93	1.74	1.68-1.8	1.57-1.92	1.86	1.79-1.93	1.66-2.09	1.80	1.73-1.88	1.59-2.04
	2012-13	1.73	1.67-1.79	1.56-1.92	1.73	1.67-1.79	1.57-1.92	1.74	1.68-1.81	1.57-1.94	1.69	1.54-1.86	1.29-2.23
	2013-14	1.63	1.57-1.68	1.47-1.81	1.63	1.57-1.68	1.47-1.8	1.53	1.47-1.59	1.37-1.71	1.57	1.42-1.73	1.18-2.1
	2014-15	1.55	1.5-1.61	1.4-1.73	1.55	1.5-1.61	1.4-1.72	1.70	1.63-1.77	1.5-1.92	1.68	1.5-1.87	1.23-2.3

Table D-3: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2001–02 fishing year for blacklip abalone (pāua; *Haliotis iris*) in New Zealand quota management area PAU 7, obtained from mandatory pāua catch effort landing return forms. CPUE indices were estimated from the year effects (base index), and include the posterior mean, interquartile range (IQR) and 95% confidence interval (CI) for each of four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects.

Index type	Fishing year	glmm			glmm sp			glmm ar			glmm sp ar		
		Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI	Mean	IQR	CI
std	2002-03	0.96	0.95-0.97	0.94-0.98	0.96	0.95-0.97	0.94-0.98	0.98	0.97-0.99	0.95-1.01	0.98	0.96-0.99	0.94-1.01
	2003-04	0.97	0.96-0.98	0.94-0.99	0.97	0.96-0.98	0.95-0.99	1.02	1.01-1.04	0.98-1.07	1.02	1-1.04	0.98-1.07
	2004-05	1.14	1.13-1.15	1.11-1.17	1.14	1.13-1.15	1.11-1.17	1.24	1.22-1.26	1.18-1.3	1.24	1.22-1.27	1.18-1.31
	2005-06	1.62	1.61-1.64	1.58-1.66	1.62	1.61-1.64	1.58-1.66	1.68	1.65-1.71	1.59-1.77	1.65	1.62-1.69	1.56-1.75
	2006-07	1.58	1.56-1.59	1.54-1.62	1.58	1.56-1.59	1.54-1.62	1.68	1.64-1.71	1.58-1.78	1.64	1.61-1.67	1.55-1.74
	2007-08	1.74	1.73-1.76	1.71-1.79	1.74	1.73-1.76	1.71-1.79	1.84	1.81-1.88	1.74-1.96	1.79	1.76-1.83	1.69-1.9
	2008-09	1.81	1.79-1.82	1.76-1.86	1.81	1.79-1.82	1.76-1.86	1.92	1.88-1.96	1.81-2.04	1.86	1.83-1.91	1.75-1.98
	2009-10	1.81	1.79-1.83	1.76-1.86	1.81	1.79-1.83	1.76-1.86	1.93	1.88-1.97	1.81-2.05	1.87	1.83-1.91	1.76-1.99
	2010-11	1.81	1.8-1.83	1.76-1.86	1.81	1.8-1.83	1.76-1.86	1.89	1.85-1.94	1.78-2.02	1.83	1.79-1.87	1.72-1.95
	2011-12	1.73	1.72-1.75	1.69-1.78	1.74	1.72-1.75	1.69-1.78	1.86	1.82-1.9	1.75-1.98	1.80	1.76-1.84	1.69-1.92
	2012-13	1.73	1.71-1.75	1.68-1.78	1.73	1.71-1.75	1.68-1.78	1.84	1.8-1.88	1.73-1.96	1.79	1.75-1.82	1.68-1.9
	2013-14	1.63	1.61-1.64	1.58-1.67	1.63	1.61-1.64	1.58-1.67	1.69	1.66-1.72	1.6-1.79	1.64	1.6-1.67	1.54-1.74
	2014-15	1.55	1.54-1.57	1.5-1.6	1.55	1.54-1.57	1.51-1.6	1.62	1.59-1.65	1.53-1.7	1.58	1.55-1.61	1.49-1.68

Table D-4: Estimates of the catch-per-unit-effort (CPUE) index relative to the 2012–13 fishing year for blacklip abalone (pāua; *Haliothis iris*) in New Zealand fishery management area PAU 7, obtained from dive data loggers. Estimates include the posterior mean, interquartile range (IQR) and 95% confidence interval (CI) for each of four models: a simple generalised linear mixed model (glmm), and GLMMs with spatial (glmm sp), temporal (glmm ar) and spatio-temporal (glmm sp ar) effects.

Index type	Fishing year	glmm				glmm sp				glmm ar				glmm sp ar			
		Mean	IQR	CI	Mean	IQR	CI	CI									
std	2013-14	0.97	0.94–1	0.88–1.06	0.96	0.93–0.99	0.88–1.06	0.96	0.93–0.99	0.87–1.05	0.95	0.91–0.99	0.85–1.06	0.95	0.81–0.89	0.75–0.97	0.85
	2014-15	0.94	0.91–0.98	0.85–1.05	0.93	0.89–0.96	0.83–1.04	0.91	0.88–0.95	0.81–1.02	0.85	0.81–0.89	0.75–0.97				
max	2013-14	0.97	0.84–1.11	0.65–1.47	0.96	0.84–1.1	0.66–1.46	0.98	0.84–1.14	0.64–1.54	0.99	0.73–1.34	0.41–2.43	0.99	0.73–1.34	0.41–2.43	0.99
	2014-15	0.94	0.82–1.08	0.64–1.44	0.93	0.81–1.07	0.63–1.41	0.94	0.81–1.1	0.61–1.49	1.05	0.77–1.42	0.44–2.56				