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Evaluation of spatiotemporal imputations for fishing catch rate standardisation

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Abstract

As commercial fishing activity shifts to target different grounds over time, spatial gaps can be created in catch rate data and lead to biases in derived indices of fish abundance. Imputation has been shown to reduce such biases. In this study, the relative performance of several imputation methods was assessed using simulated catch rate datasets. Simulations were carried out for three fish stocks targeted by a commercial hook and line fishery off the south-western coast of Australia: Snapper (*Chrysophrys auratus*), West Australian Dhufish (*Glaucosoma hebraicum*), and Baldchin Groper (*Choerodon rubescens*). For High Growth scenarios, the mean squared errors (MSEs) of Geometric and Linear imputations were lower, indicating higher accuracy and precision, than Base method (constant value) imputations. For Low Growth scenarios, the lowest MSEs were achieved for Base method imputations. However, for the final standardised and imputed abundance indices, the Base method index consistently demonstrated the largest biases. Results demonstrate the importance of selecting an appropriate imputation method when standardising catch rates from a commercial fishery that changed its spatial pattern of fishing over time.

Introduction

Conventional statistical methods, including generalized linear models (GLMs), are routinely used to standardize commercial catch-per-unit-of-effort (CPUE) data into indices of relative fish abundance for stock assessment. However, missing CPUE data from some areas and times often occurs due to the highly mobile nature of commercial fishing and can lead to biases in the resulting indices of fish abundance. The use of suitable imputation methods, such as those recommended by Walters (2003), have proven useful for reducing such biases.

However, despite the frequency and importance of this issue the performance of alternative CPUE imputation models (in the absence of relevant auxiliary data; see Ono et al, 2015) has not been investigated. The model suggested by Walters (2003), referred to in this paper as the Base method, imputes a constant value for each period of missing data. The imputed value is based on conventional rules for imputation, including taking the mean value, nearest neighbour (i.e., in time) and last observation carried forward (LOCF). Walters (2003) demonstrated that his imputations reduced an apparent bias that manifested in an initial rapid decline in CPUE. The steepness of this initial decline was likely reflecting localized effects of fishing on fish population abundance as opposed to stock-wide trends. This effect is more generally known as hyperdepletion (Hilborn and Walters 1992).

More recently, Carruthers et al. (2011) used simulations to demonstrate how Base method imputations could be incorporated into a statistical CPUE standardisation using GLMs. Importantly, this method accounted for the prospect that the trend of

CPUE may be different in different areas. As such, this is an improvement over more conventional spatial imputation procedures such as kriging (Matheron 1963; Isaaks and Srivastava 1989). Ono et al. (2015) also used simulations to evaluate Base method imputations and found that the incorporation of ancillary data, such as from Baited Remote Underwater Video (Bornt et al. 2015; McLaren et al. 2015) or diver surveys (Russ and Alcala 1998; Russ et al. 2003), could result in less biased imputations for U.S. groundfish species. However, for many fisheries CPUE datasets, such ancillary data are often not available when CPUE data are missing.

The aim of this study is to evaluate the effectiveness of several alternative imputation methods for use in CPUE standardisation against the Base (i.e., constant imputed value) method, for predicting historical trends in relative abundance, in cases where no ancillary data are available for informing imputations. Each of the alternative imputation methods is a simple empirical function calculating the trend of imputed values (Linear, Geometric, Negative Exponential, Logistic). Simulations are used to evaluate imputation method performance for the CPUE of three species targeted by the commercial hook and line fishery off the west coast of Australia: Snapper (*Chrysophrys auratus*), West Australian Dhufish (*Glaucosoma hebraicum*), and Baldchin Groper (*Choerodon rubescens*). This fishery is presently the West Coast Demersal Scalefish Interim Managed Fishery (WCDSIMF), which comprises approximately 60 licensed fishing vessels that have collectively landed over 300 tonnes of demersal scalefish each year, since 2008 (Fig. 1, Fairclough et al. 2014*a*). Prior to the commencement of the WCDSIMF, commercial operators harvested demersal scalefish from these grounds using hook and line gear, as part of the statewide open-access “wetline” fishery (Wise et al. 2007). The performance of the

Base and alternative imputation methods is evaluated by comparing trends in imputed values against population trajectories, mean squared errors of the imputed values, and derived indices of fish abundance.

Materials and methods

Overview

The simulation model was designed to generate catch and effort data with similar properties to historical logbook data reported to the Department of Fisheries, Government of Western Australia (DoFWA) by commercial hook and line fishers operating in these waters since 1975 (Wise et al. 2007). Simulated catch and effort data were generated for each vessel's activities within each grid block of ocean, delineated by degree lines of latitude and longitude ($60'$ blocks), over a 30-year time period. Fish population and fishery dynamics were simulated over finer spatial scales ($10'$ blocks), with alternative scenarios run for different levels of population growth rate and fishing depletion, types of adult movement, and spatial autocorrelation (Fig. 1). The fleet was subdivided into several non-overlapping "management areas", to emulate the relatively localized patterns of fishing by each vessel and recently implemented (i.e., since 2008) spatial entitlements (Crowe et al. 1999; Marriott et al. 2011; Fairclough et al. 2014*a*). Stochasticity was incorporated using Monte Carlo resampling for 200 model iterations, within each of 24 simulated scenarios (Table 1).

Missing data were created for randomly selected $60'$ blocks by specifying that commercial fishing did not occur for one of three time periods (Years 1—10; Years 11—20; Years 21—30). A matrix of estimated marginal means (EMMs; Searle et al. 1980), for combinations of $60'$ block with year, was then predicted from a GLM fitted to these data. The Base method and four alternative imputation methods were applied to fill in those cells corresponding to the missing data. Imputed EMM matrices were converted into indices of abundance by averaging across the levels of block within each year and then compared against the trajectory of simulated population abundance to assess the relative performance of each method.

Model inputs: data and parameter estimates

Commercial catch and effort data were obtained from statutory fishing returns submitted to the DoFWA by licensed operators in the WCDSIMF for the calendar years 2008—2014. The fishing returns reported catch and effort for sessions of fishing lasting not more than 24 hours within $10' \times 10'$ blocks for every trip completed by each vessel. These logbook returns have recently (i.e., since 2008) been implemented to replace the historic Catch And Effort System (CAES) returns, upon which monthly summaries of catch and effort within $60'$ blocks had been reported (Crowe et al. 1999; Marriott et al. 2011).

Records with nonzero catches of the study species from the first year of data collection (2008) and $10'$ blocks with $n > 3$ catch records were identified as spatial population sub-units and included in preliminary analyses. There were n_a sub-units identified for each stock (Table 2). Local spatial population distributions were assumed to be represented by these blocks, except for outlying blocks, which did not share adjacent boundaries and were excluded (4.1 % of $10'$ blocks for Snapper; 3.1 % for Baldchin Groper; 2.3 % for Dhufish). As commercial fishing for demersal scalefish was prohibited in the Metro zone management area of the WCDSIMF (31–33°S) in 2008, the spatial distribution of charter fishing catches of Dhufish from

1 July 2002—30 June 2003, as reported in Wise et al. (2007), were used to define population sub-units for the corresponding simulated management area (m_4: Fig. 1).

Explanatory variables were selected and linear mixed models (LMMs) fitted to log-transformed CPUE data following the methods of Fairclough et al. (2014*b*). Crossed random effects terms were estimated for $10'$ blocks (intercept) and vessels (intercept). The estimated variance component for residual errors was taken as an estimate of the variation within groupings of $10'$ block and vessel. These estimates were converted into dimensionless coefficients of variation (s_a, s_v, s_ϵ) by dividing the square root of each estimate by the mean of the response. These values were multiplied by the respective mean of the log-transformed simulated quantity and then squared to obtain the rescaled estimates of variance ($\mathrm{Var}[\log(\bar{N}_{\cdot,0})]$, $\mathrm{Var}[\log(C_v)]$, $\mathrm{Var}[\epsilon_{v,a,y}]$)[1].

Available information on the population dynamics of Snapper, Dhufish and Baldchin Groper (Lenanton et al. 2009; Anon 2010; Fairclough et al. 2011; Wakefield et al. 2011), were also used to obtain estimates for simulation model parameters[1]. An initial assumed value for the rate of population growth proportional to population size ($r = r_{\mathrm{init}}$) was the value of r from the discrete logistic model for population growth which resulted in a close approximation to the projected recovery trend of N_y, from $N_1 = 0.05N_0$ to N_{30}, as calculated from a single-sex age-structured model (R. J. Marriott unpublished data). As this calculated r_{init} was a highly uncertain estimate, a single "Low Growth" ($r_{\mathrm{init}} - 2\hat{\sigma}_r$) and "High Growth" ($r_{\mathrm{init}} + 2\hat{\sigma}_r$) input value was used for each stock, where $\hat{\sigma}_r = \sqrt{\mathrm{Var}[r_{\mathrm{init}}]}$. This was done so that the influence of

[1] Refer to Supplementary Data for details.

these different *r* inputs, representing plausible lower and upper bounds for its uncertainty, could be evaluated in simulated scenarios.

The model

Fish stocks were simulated as closed populations with density-dependent population growth according to the following model:

(1)

$$N_{a,y}^{\text{grow}} = N_{a,y} + N_{a,y}\left(b_{\max} - \frac{b_{\max} - d_{\min}}{2N_{a,0}}\bar{N}_{\cdot,y}\right) - N_{a,y}\left(d_{\min} + \frac{b_{\max} - d_{\min}}{2N_{a,0}}N_{a,y}\right),$$

(2)

$$N_{a,y+1} = \min\left(N_{a,y}^{\text{grow}} - \textstyle\sum_v C_{v,a,y} + N_{a,y}^{\text{move}},\ N_{a,0}\right),$$

where: $N_{a,y}$ is the number of fish in population sub-unit *a* and year *y*; $b_{\max}$ and $d_{\min}$ are the respective birth and death *per capita* rate processes at very low population sizes ($r = b_{\max} - d_{\min}$); $\bar{N}_{\cdot,y} = \frac{1}{n_a}\sum_a N_{a,y}$ is the mean number of fish per sub-unit in year *y*; $\sum_v C_{v,a,y}$ is the number of fish removed due to fishing by all vessels (*v*) in the fleet from sub-unit *a* in year *y*; and $N_{a,y}^{\text{move}}$ was the net number of fish immigrating to sub-unit *a* from adjacent sub-units. Equation (1) was a reformulation of the discrete form of the logistic population growth model, assuming simple linear density-dependence in the population birth and death rates (Pianka 1974)[2]. This model takes into account the two-stage life histories known for the study species, which involve a highly mobile (pelagic) larval phase and a more sedentary (benthic) post-larval and adult phase (Francis 1994; Berry et al. 2012; Gardner et al. 2015). The second term in Equation (1) represents contributions (i.e., recruitment) due to density-dependent birth rates, where density-dependent effects are determined by the average of population

[2] Refer to Appendix A for derivation.

densities, across all population sub-units in year *y*. The third term represents losses due to more localised density-dependent death rates (i.e., natural mortality), within that population sub-unit in year *y*. Equation (2) shows that the numbers of fish changed from year *y* to *y*+1 due to assumed density-dependent *per capita* rate processes ($N_{a,y}^{\text{grow}}$), followed by removals due to fishing ($\sum_v C_{v,a,y}$), and then fish movements among adjacent sub-units ($N_{a,y}^{\text{move}}$)[3]. For the Diffusion and DDHS (MacCall 1990) scenarios (not reported here[3]), $N_{a,y}^{\text{move}}$ took either positive (net immigration) or negative (net emigration) values, otherwise $N_{a,y}^{\text{move}} = 0$. A simplifying assumption was that the $N_{a,y}$ could not exceed the initial pre-fishing abundance for that sub-unit, $N_{a,0}$.

Catches by each vessel from each sub-unit and year were calculated accordingly:

(3)

$$C_{v,a,y} = \min\left(\sum_i q_v\, E_{i,v,a,y} N_{a,y}, 0.95 N_{a,y}\right) \epsilon_{C'}$$

where: q_v is the catchability coefficient for vessel *v*; $E_{i,v,a,y}$ is the unit of fishing effort expended by vessel *v* during fishing event *i* within that sub-unit and year; and $\epsilon_{C'}$ is the lognormally distributed error term explaining the variability in catches among fishing events for each vessel within sub-units. The constraint that no more than 95 % of the sub-unit abundance could be caught was imposed to exclude the unlikely situation where all of the fish are caught by a vessel within a single year. For simplicity, for the entire fleet and across management areas, $E_{i,v,a,y} = 1$ and $\sum_{i,v,a} E_{i,v,a,y} = n_a$, with the level of simulated catch scaled by an input harvest ratio parameter (*H*) and q_v. Fishing by all vessels was simulated as a single event within

[3] Refer to Supplementary Data for details.

each time step, with each vessel constrained to operate within one of three (Snapper and Baldchin Groper: m_1, m_2, m_3) or four (Dhufish: m_2, m_3, m_4, m_5) simulated management areas (*m*; Fig. 1). The number of vessels allocated to each *m*, as a proportion of the simulated fleet size, was commensurate with the number of population sub-units within that *m*, as a proportion of the total number n_a (Table 2). For simplicity, we assumed the spatial and temporal patterns of other sources of fishing mortality (e.g., from recreational catches) demonstrated the same patterns as those simulated for commercial fishing mortality.

An input value for the average harvest ratio in Year 15, *H*:

(4)

$$H = \frac{\bar{C}}{\bar{N}_{\cdot,15}\bar{W}n_a}$$

was the (model-tuned) value that resulted in a level of relative depletion by Year 30:

(5)

$$D\ (\%) = 100\ \times \frac{\sum_a N_{a,30}}{\sum_a N_{a,0}}$$

that was within 1 of the pre-specified level for *D*. The $\bar{N}_{\cdot,15}$ in Equation (4) is the average simulated sub-unit abundance in Year 15 and $\bar{C}$ (average annual commercial catch), $\bar{W}$ (mean fish weight), and n_a are fixed model inputs (Table 2). Two alternative values for *D* were simulated: *D* = 50 % (*Moderate Depletion*) and *D* = 25 % (*High Depletion*). The High Depletion scenario corresponded to a level that was between the DoFWA's Threshold and Limit Reference levels (Wise et al. 2007), indicating an unsustainable level of fishing. The Moderate Depletion scenario simulated a stock abundance that was double the High Depletion level for Year 30 and was above the DoFWA's Target Reference level (Wise et al. 2007), indicating a sustainable level of fishing.

Stochastic processes

Two hundred Monte Carlo iterations were run for each scenario. The pre-fishing abundance in each sub-unit and vessel-specific catchability coefficients were calculated by sampling once, for each Monte Carlo iteration, from the respective parametric distributions:

(6)

$$\log\left(N_{a,0}\right) \sim \mathrm{Normal}\left(\log\left(\bar{N}_{\cdot,0}\right), \mathrm{Var}\left[\log\left(\bar{N}_{\cdot,0}\right)\right]\right)$$

(7)

$$\log\left(q_v \bar{E}_{\cdot,\cdot,15} \bar{N}_{\cdot,15}\right) \sim \mathrm{Normal}\left(\log\left(\bar{C}_{\cdot,\cdot,15}\right), \mathrm{Var}[\log(C_v)]\right)$$

where: $\bar{N}_{\cdot,0} = 2\bar{N}_{\cdot,15} \,/\, (1 + D/100)$ is the average starting abundance per sub-unit; $\log(\bar{C}_{\cdot,\cdot,15}) = \log(\bar{N}_{\cdot,15} H_C) - \log(\bar{n}_V)$ is the logged mean catch per vessel per sub-unit per year; $H_C = P_C H$ is the commercial harvest ratio; $\bar{n}_V = \sum_v n_V \,/\, n_m$ is the average number of vessels per management area; $\bar{E}_{\cdot,\cdot,15} = \sum_{v,a} E_{v,a,15}/n_a = 1$; and P_C, n_V, n_m are fixed model inputs (Table 2). Each q_v was obtained from Equation (7) after Monte Carlo sampling by exponentiation and then dividing by $\bar{N}_{\cdot,15}$. The $E_{i,v,a,y}$ to be expended by each vessel within each respective management area m were randomly allocated among sub-units each year by resampling from a multinomial distribution, parameterised using a deterministic probability vector ($p_{a,y}$). Each $p_{a,y}$ was directly proportional to the available $N_{a,y}$ prior to fishing (i.e., $p_{a,y} = N_{a \in m,y} / \sum_{a \in m} N_{a,y}$), following Little et al. (2011). In addition, variability among the catches of each vessel from each sub-unit in each year in Equation (3) was simulated by resampling from:

(8)

$$\log(\epsilon_{C'}) \sim \mathrm{Normal}(0, \mathrm{Var}[\epsilon_{v,a,y}]) \quad .$$

The period when missing data occurred determines the type of calculation required for imputation (e.g., Walters 2003). Following Walters (2003), we named these three different types of missing data periods: (i) *Before*: data missing at the start of a CPUE data series; (ii) *After*: data missing from the end of a series; (iii) *Gap*: period of missing data, which is neither the Before or After type. Three $60'$ blocks were randomly selected, without replacement, to have one of these missing data patterns, so that each type was represented once in each model iteration. The simulated missing data patterns were: Before period (Years 1—10); Gap period (Years 11—20); After period (Years 21—30). Ten years was selected as the time period to simulate missing data because this was judged to be sufficiently long to detect possible effects of imputation, but not excessively long when compared to the age of most fisheries. Candidate $60'$ blocks for simulating missing data were those with at least 10 sub-units because these were considered likely to generate sufficient CPUE observations to use for imputing the missing values. The mean ($\pm$ SE) size of the imputed area, as a proportion of simulated stock area, was 0.16 ($\pm$ 0.06) for Snapper and Baldchin Groper, and 0.12 ($\pm$ 0.04) for Dhufish (High Growth High Depletion scenarios).

Standardisation model and imputations

An overdispersed poisson GLM was selected for fitting to simulated catches in numbers ($C_{k,v,y}$) from each Vessel (v), Year (y), and $60'$ block (*Block*; k), with log-transformed effort ($\log E_{k,v,y}$) modeled as an offset variable, following guidelines of Maunder and Punt (2004):

(9)

$$\log\left(\mathbb{E}\left[C_{k,v,y}\right]\right) = \beta_0+\beta_{1,v}X_{1,v}+\beta_{2,k}X_{2,k}+\beta_{3,y}X_{3,y}+\beta_{4,k,y}X_{2,k}X_{3,y}+\log\left(E_{k,v,y}\right) .$$

The dispersion parameter was estimated to account for the prospect of over-dispersion in the simulated CPUE datasets (O'Neill et al. 2011; Marriott et al. 2014). A matrix of EMMs, for observed combinations of $60'$ block against year, were predicted using the fitted GLM.

Five methods were applied to fill in those cells corresponding to missing data in this Block × Year matrix of EMMs (Table 3). These were the *Base* method, which is equivalent to the method used by Walters (2003) and Carruthers et al. (2011), and four other non-Base methods. Each method used observed EMMs (inferred $I_{k,y}$) for the *k*th Block to calculate imputed values ($\dot{I}_{k,y}$) to replace the missing EMMs for that Block.

Imputation calculations also varied according to the type of missing data period (Before, Gap, After). The Base method imputed a constant value for each type: Before type imputed values $\dot{I}_{k,y}$ are the mean of the first three observed $I_{k,y}$ (i.e., $\frac{1}{3}\sum_{y=11}^{13} I_{k,y}$); Gap type $\dot{I}_{k,y}$ are the mean of the $I_{k,y}$ preceding and following the gap (i.e., mean$(I_{k,10}, I_{k,21})$); After type $\dot{I}_{k,y}$ are the last observed $I_{k,y}$ in the series (i.e., $I_{k,20}$) (Walters 2003). The non-Base methods are empirical functions calculating alternative trends for the imputed $\dot{I}_{k,y}$: *Linear*, *Geometric*, *Negative Exponential* and *Logistic*. The Linear method is the simplest for imputing changing relative abundance in the absence of fishing, although it may not be biologically realistic. Geometric and Logistic method imputations are consistent with the shape of typical density-independent and density-dependent recoveries in population abundance in the absence of fishing, respectively. Imputations by the Negative Exponential method mirror those of the Geometric method, and have been included for completeness. (Table 3)

The non-Base methods use a value for the year (y=A) preceding, or at the commencement of, the missing data (Before: $\dot{I}_{k,A} = \frac{1}{3}\sum_{y=11}^{13} I_{k,y}$; Gap: $I_{k,A} = I_{k,10}$; After: $I_{k,A} = I_{k,20}$) and for the year (y=B) following or ending that missing data period (Before: $I_{k,B} = I_{k,11}$; Gap: $I_{k,B} = I_{k,21}$; After: $\dot{I}_{k,B} = I_{k,A} + \dot{\beta}_{\mathrm{Gap}}(B - A)$) to map the respective imputation function to the observed $I_{k,y}$ (Table 3). For the After type imputations, the $\dot{\beta}_{\mathrm{Gap}}$ is calculated to use information in the available $I_{k,y}$ (i.e., the linear rate of change in $I_{k,y}$ either side of Gap missing data) to extrapolate the $\dot{I}_{k,B}$. Occasionally missing values arose for $60'$ blocks outside of the simulated 10-year missing data periods due to random chance. In those cases, imputations were done using the same method, to result in fully imputed Block × Year matrices.

Imputed EMM matrices were converted into indices of abundance by averaging across the levels of Block within each Year (Punt et al. 2000). Indices were also generated for standardised CPUE calculated without imputation (*No Impute* method), and as predicted from the fitted GLM omitting the interaction term with no imputations (*Main Effects* method). Residuals from the fitted GLM were bootstrapped 1,000 times to calculate the variances of the log-transformed imputed values, as well as the bias-adjusted 95 % confidence intervals for each index of abundance, following Marriott et al. (2014).

Evaluating imputation methods

The $\dot{I}_{k,y}$ and $N_{k,y}$ for each $60'$ block and year were normalised so that the trends in imputed indices versus population abundances could be visually compared on plots at the same scale, for each type (Before, Gap, After) and method of imputation. Normalised values for the $\dot{I}_{k,y}$ were calculated by dividing by the mean of the observed $I_{k,y}$ used for Base method imputations (i.e., divide the $\dot{I}_{k,y}$ by: $\frac{1}{3}\sum_{y=11}^{13} I_{k,y}$ for Before imputations; $\text{mean}(I_{k,10}, I_{k,21})$ for Gap imputations; or $I_{k,20}$ for After imputations; Table 3). Normalised values for the $N_{k,y}$ population abundances were calculated in a similar manner (e.g., divide the $N_{k,y}$ to be compared with normalised Before type $\dot{I}_{k,y}$ by $\frac{1}{3}\sum_{y=11}^{13} N_{k,y}$). Although plots for all scenarios are available[4], only those for High Growth, High Depletion are presented here, as the *a priori* expectation was that this simulated state would demonstrate the greatest contrasts in $N_{k,y}$.

Log-transformations were done to transform imputed CPUE with assumed multiplicative error structure into values with assumed additive errors for calculating mean squared errors (MSEs). The MSE of the logged $\dot{I}_{k,y}$ was calculated for each type and method to measure relative performance:

(10)

$$\text{MSE}\left(\log(\dot{I}_{k,y}+1)\right) = \text{Bias}^2\left(\log(\dot{I}_{k,y}+1)\right) + \text{Var}\left(\log(\dot{I}_{k,y}+1)\right) ,$$

where:

(11)

$$\text{Bias}\left(\log(\dot{I}_{k,y}+1)\right) = \log(\dot{I}_{k,y}+1) - \log(O_{k,y}+1) \;;$$

[4] Refer to Supplementary Data for plots of other simulated scenarios.

$\mathrm{Var}(\log(\dot{I}_{k,y}+1))$ was the variance of the log-transformed bootstrapped values for $\dot{I}_{k,y}$; and the $O_{k,y}$ values were the corresponding $N_{k,y}$ that had been transformed to the same scale as the $\dot{I}_{k,y}$. MSE values were averaged across years to provide an overall measure of the relative accuracy and precision of imputed values for each type and method (i.e., average MSE).

Results

Trends and biases in imputed values

Graphs of normalised imputed values against normalised population abundances demonstrate that some imputed indices reflect better the underlying trend of localised (i.e., within $60'$ blocks) abundances than others during missing data (no fishing) periods (Fig. 2). The relative precision of mean imputed values (not shown) was generally lower for Baldchin Groper than for Snapper and Dhufish, reflecting the higher level of stochastic variation used to simulate Baldchin Groper abundances and CPUE (specified using s_a, s_v, s_ϵ; Table 2). Before type imputations underestimated normalised relative abundances for all stocks, with clear differences between imputed trends when comparing the Base method with the other (non-Base) methods. Greater variation was apparent among the non-Base methods for Gap and After type imputations than for Before type imputations (Fig. 2).

Before type imputations by the Base method underestimated the normalised abundance trend by a constant amount, on average (Fig. 2). However, the non-Base methods demonstrated a gradual reduction in this bias from Years 1 to 10 of the missing data period. These patterns were also demonstrated for Before type imputations in other scenarios (Low Growth, High Depletion; High Growth, Moderate Depletion; Low Growth Moderate Depletion), with smaller biases apparent for scenarios with Low Growth (r), Moderate Depletion (D), or both[5].

Population abundances for $60'$ blocks and periods with no fishing were observed to recover from previously depleted states during Gap (Years 11-20) and After (Years 21-30) missing data periods (Fig. 2). The gradual increase in Linear and Logistic Gap type imputations with year more closely approximated relative abundance than Base and Negative Exponential Gap type imputations. Gap type imputations by the Geometric method better approximated relative abundances for Snapper and Dhufish than for Baldchin Groper for the High Growth, High Depletion scenario (Fig. 2), but this result was variable among the other simulated scenarios[5].

Similar population trajectories were observed among stocks during the After missing data periods for the High Growth, High Depletion scenario (Fig. 2). The Base method underestimated relative abundances by an increasing amount in later years, whereas the non-Base methods overestimated relative abundances to a greater extent in later years. This difference between methods was apparent in all other scenarios, except in cases where population abundances did not recover as much during the missing data period, such as in some of the Moderate Depletion scenarios simulated for Snapper and Dhufish[5].

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[5] Refer to Supplementary Data for details.

Mean Squared Errors of imputed values

Medians of the average MSEs were consistently lower for imputations of Snapper and Dhufish standardized CPUE than for Baldchin Groper (Fig. 3). This indicated better average performance of imputations for Snapper and Dhufish than for Baldchin Groper, in terms of the accuracy and precision for imputations matching relative abundances. Medians of the average MSEs were also generally lowest for Before type imputations and highest for After type imputations (Fig. 3). Furthermore, although truncated axes omit outliers, or upper whiskers, or both from some of these plots, the relatively high variation in average MSEs is readily apparent. This reflects simulated levels of stochastic variation within each of the scenarios.

Across all scenarios and types of imputation, medians for the Base method were lowest (indicating best performance) in the majority of cases (Table 4a). However, there was also a conspicuous influence of the selected level for r on results. For most of the Low Growth scenarios, Base method imputations had the lowest medians of average MSE, but for most of the High Growth scenarios Geometric or Linear imputations demonstrated the lowest medians (Table 4a). The effect of D, although less pronounced than that of r, was also apparent. In Moderate Depletion scenarios Base method imputations most often had the lowest median but in High Depletion scenarios Geometric imputations most often had the lowest median (Table 4a).

Aside from the High Growth High Depletion scenarios, the Base method consistently demonstrated the lowest median of average MSE for Before type imputations (No Movement scenarios; Fig. 3, Table 4b). However, for Gap and After type imputations, in most cases (and especially for High Depletion scenarios) the Geometric or Linear methods produced the lowest medians of average MSE (Table 4b). The Base method produced the lowest medians for Gap and After type imputations done in Moderate Depletion scenarios simulated for Dhufish and for Gap type imputations of Low Growth Moderate Depletion scenarios simulated for Snapper and Baldchin Groper. It is important to acknowledge, however, the relatively wide variation in values above and below some of these medians, and in some cases, the relatively small differences between them (Fig. 3).

Indices of abundance

At the stock level, the initial decline in normalised I_y in simulation Years 1–10 was greater than the corresponding decline in normalised N_y, indicating an effect of hyperdepletion in indices of abundance for High Growth, High Depletion scenarios with No Movement (Fig. 4). However, this hyperdepletion bias was reduced for all imputed indices. Hyperdepletion biases for each method are more clearly shown on plots of mean relative error ($RE_y = \log(\text{normalised } I_y) - \log(\text{normalised } N_y)$) as a declining mean RE_y with year (i.e., as compared to the horizontal line for relative abundance, $\text{mean}(RE_y) = 0$; Fig. 5). The sharp increases in mean RE_y from Years 10 to 11 and 20 to 21 correspond with unstandardised increases in CPUE following effort shifts into $60'$ blocks that had not been fished for the previous 10 year period.

Hyperdepletion biases were most conspicuous from Year 3 to 10, from Year 12 to 20, and from Year 22 to 30, for the Main Effects, No Impute, and Base method indices (High Growth, High Depletion, No Movement scenarios, Fig. 5). The pattern of mean RE_y was generally more stable, and closer to zero in the final year, for non-Base methods than for the Base method (Fig. 5). A lower negative mean RE_{30} for the Base method indicates that estimates of relative abundance for that final year would be more negatively biased than those from non-Base methods. This larger average (negative) relative error for the Base method in Year 30 was consistent across all other scenarios, although the relative differences in the mean RE_{30} between methods was variable[6].

Discussion

Simulation evaluations demonstrated that, in some cases, alternatives to the Base method of Walters (2003) could result in a reduced bias and an increased precision of imputed standardised CPUE. Geometric and Linear imputations were more accurate and precise than Base method imputations in High Growth scenarios, but the Base method imputations were more accurate and precise in Low Growth scenarios. An effect of the specified level of relative depletion (although less pronounced than that of specified growth) also influenced the relative accuracy and precision of different imputations. However, in all scenarios, imputed indices of stock abundance demonstrated lower biases than non-imputed indices, which was consistent with results from other studies (Walters 2003; Campbell 2004; Carruthers et al. 2011; Ono et al 2015). The Main Effects (no Block × Year interaction and no imputation) index demonstrated the largest hyperdepletion biases and underestimated relative abundances in the final year by the largest amounts. Of the imputed indices, the Base method index demonstrated the largest biases, and these results were found to be consistent in other simulated movement and spatial autocorrelation scenarios not

6 Refer to Supplementary Data for details.

presented[7]. These results demonstrate that standardisation of CPUE sampled from a commercial fishery that changed its spatial pattern of fishing over time requires two key steps, in order to obtain accurate and precise results: (i) a spatial factor by year interaction term; and (ii) an appropriate imputation model.

This study used a simulation model tailored to generate CPUE data with missing observations for demersal scalefish species caught by the WCDSIMF. However, although aspects of model structure were specific to this fishery, many simplifying assumptions were made, in order to elucidate those more general phenomena concerning CPUE imputations (Roughgarden 1998). Accordingly, we believe that these results should be transferable to other studies, and particularly for those fisheries that target demersal scalefish with pelagic larval dispersal and more site-attached adult life stages. In addition, the study species are monitored as indicators for assessing and managing the suite of demersal scalefish species harvested by the WCDSIMF (Wise et al. 2007; Anon 2011; Fairclough et al. 2014*a*). Therefore, results should be relatively robust to possible future changes of indicator species, or uncertainties in more species-specific (e.g., age-based) life history processes not simulated.

Other simulation studies have selected different mechanisms for generating the missing CPUE. Campbell (2004) modeled random effort distribution and spatial contraction as candidate exploitation patterns to generate missing observations. More recently, Campbell (2015) simulated a dataset for imputation using parameter estimates from a delta-GLM fitted to a subset of commercial broadbill swordfish

[7] Refer to Supplementary Data for details.

CPUE with one missing year × quarter × region stratum. Carruthers et al. (2011) simulated age-structured fish population dynamics and imposed fishing dynamics including hyperstability and hyperdepletion scenarios, which related to shifts in targeted effort towards or from different species. Ono et al. (2015) included hyperstable and hyperdepleted ancillary data to use for imputations, with missing CPUE occurring due to the simulated creation of marine reserves. These different mechanisms were more or less specific to each simulated fishery, and thus created particular types of missing data pattern to explore effects of CPUE imputations.

This study generated missing observations by randomly selecting areas to simulate each of three different types of missing data period. This excluded the potentially important (but unknown) influence of historical increases effective fishing effort, as identified from a survey of past and current skippers (Marriott et al. 2011). It also assumed that any effect from other sources of fishing mortality (e.g., from recreational fishing), acting upon fish in locations where and when there were missing data, was negligible. In addition, in all scenarios steeper declines were observed for the resulting standardised indices than in population trajectories, reflecting an underlying hyperdepletion in the simulated CPUE. However, the presented simulation facilitated balanced comparisons of imputation methods, for each scenario and type of imputation calculation (Before, Gap, After), across 200 different hypothetical missing data patterns. Furthermore, as the comparisons were done across a wide variety of simulated missing data patterns, this lends support to the extension of presented findings to other fisheries with different spatiotemporal patterns of missing CPUE.

Various methods have been proposed to address biases arising due to spatial gaps in the CPUE datasets. Campbell (2004) proposed a method that uses the mean or maximum of values predicted from the statistical model fitted to CPUE for other fished regions or grid blocks in that year to impute the missing values. More recently, Campbell (2015) has proposed a range of other imputation methods. One, called the "infill" method, involves fitting a delta-GLM, with all higher-order interactions of time with year, to a subset that excludes years with missing data. For each year, the ratios of standardised CPUE predicted for a spatial unit requiring imputation, to each of the other spatial units, are calculated. The mean of the ratios for that spatial unit is then rescaled for the main effect of year and used to impute the corresponding missing value in the complete dataset. Other methods proposed by Campbell (2015) involve fitting the delta-GLM without the higher order interactions of time with year and then predicting the missing value from the fitted model.

Alternative approaches by Walters (2003) and Carruthers et al. (2011) address this problem by assuming a value for areas with missing data that is independent of the values in the fished areas. Using a value that is independent of the values in the fished areas is appropriate because localised effects of fishing on abundances in fished areas may not be representative of abundance trends in the missing data areas (Walters 2003). The results from this study, however, have shown that local abundances in areas without CPUE may not be static. Therefore, imputing using values from fished areas, or using a constant value independent of the fished areas (e.g., as in the Base method), may not be optimal for reducing biases that might arise due to missing CPUE.

The approach by Ono et al. (2015) to use ancillary data from the missing data areas to impute is an improvement upon the constant value imputations because it allows for the prospect of changing abundances in those areas with missing CPUE. This method is also ideal because imputations are informed by known changes in localised abundance within those areas. Indeed, the resulting ancillary data-imputed index was shown to have reduced biases when compared to the constant value-imputed index for simulated datasets in that study (Ono et al. 2015).

However, the difficulty with the Ono et al. (2015) method is that it requires ancillary data from the areas with missing CPUE to be available. Carruthers et al. (2011) suggested that, in such cases, abundances in missing year-strata could be predicted within an integrated spatially structured population dynamics model. Another approach is to use information in the available CPUE data, plus a biologically plausible function for changing localised fish abundance (e.g., Geometric), to impute the missing values. In many of the presented simulations, this latter approach was shown to be superior in reducing these biases, as compared to the constant value (i.e. Base) imputation method.

The choice of method to use for calculating an index of abundance should be influenced by characteristics of available data, as well as fishery-specific considerations (Campbell and Tuck 1996 *in* Campbell 2004). Accordingly, such considerations should also extend to the selection of an appropriate method for imputing missing CPUE. Firstly, some understanding into the nature (and ideally the cause) of missing observations should be sought. For instance, some management changes, such as introducing fishing effort quotas or marine reserves, might shift commercial fishing effort away from some areas. In these instances, one of the non-Base methods might be suitable because local abundances would be expected to recover in areas no longer fished. However, if missing CPUE arose due to some process that affects localised abundances in unknown ways (e.g., the reallocation of commercial fishing to some other type of extractive activity), it might be prudent instead to expend available resources into the collection of ancillary data for making imputations, following Ono et al. (2015). Secondly, as there was an important effect of *per capita* population growth rate (r) on the relative bias and precision of imputations, prior knowledge of this parameter could be useful. If r is considered likely to be towards the upper end of the range simulated for this study (i.e., 0.05–0.45), then Geometric or Linear imputations would be preferable to those from the Base method, based on the presented simulations. A third (but not the last) important consideration is the spatial scale and length of time over which imputations will be done. Campbell (2004) suggests that imputations should always be done at the finest spatial scale possible and Ono et al. (2015) demonstrated that imputing across a larger proportion of the sampled stock area is likely to increase the amount of bias reduction. However, Carruthers et al. (2011) point out that imputing over very fine spatial scales may lead to biased imputations from values estimated with low sampling precision due to smaller average sample sizes per spatial unit.

Imputing over relatively long time periods could also be problematic, particularly for Before and After type imputations, which extend outside of the year range for which CPUE had been observed. This is clearly not ideal and is analogous to extrapolation, which is an unsafe form of model prediction (e.g., Ramsey and Schafer 1997; Zar 1999; Faraway 2005). Although the presented simulations imputed missing CPUE across relatively long time periods (10 years), in no cases did imputations fall outside of the observed range of CPUE. However, implausible After type imputations (e.g., very large or negative values) may be calculated when done over a relatively long time period, or when using relatively high or negative values calculated for $\dot{\beta}_{\mathrm{Gap}}$ (Table 3), or both.

Missing CPUE may be an important consideration for future assessments of these species in the WCDSIMF in light of recent (i.e., since 2008) changes to spatial management arrangements, which have resulted in the prohibition of commercial fishing from some areas. Although recent assessments have focused on monitoring performance indicators within each management area (e.g., Fairclough et al. 2014*a*; Fairclough et al. 2014*b*), the spatial distribution of each stock traverses several. Thus, if an index of stock-wide abundance is sought, such as for the purpose of incorporating into an integrated age structured stock assessment model, some strategy for dealing with a lack of information from closed areas will be required.

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Tables

Table 1. Simulation model scenarios. Movement = simulated fish movements among adjacent spatial population sub-units (10′ blocks); DDHS = Density-Dependent Habitat Selection (MacCall 1990). ** = Not reported here[8].

Scenario	Stock	Movement	Spatial Autocorrelation	Growth	Depletion Year 30
1	Snapper	None	No	Low	$0.25N_0$
2	Snapper	None	No	Low	$0.50N_0$
3	Snapper	None	No	High	$0.25N_0$
4	Snapper	None	No	High	$0.50N_0$
5	Snapper	Diffusion **	No	Low	$0.25N_0$
6	Snapper	Diffusion **	No	Low	$0.50N_0$
7	Snapper	Diffusion **	No	High	$0.25N_0$
8	Snapper	Diffusion **	No	High	$0.50N_0$
9	Snapper	DDHS **	No	Low	$0.25N_0$
10	Snapper	DDHS **	No	Low	$0.50N_0$
11	Snapper	DDHS **	No	High	$0.25N_0$
12	Snapper	DDHS **	No	High	$0.50N_0$
13	Baldchin Groper	None	No	Low	$0.25N_0$
14	Baldchin Groper	None	No	Low	$0.50N_0$
15	Baldchin Groper	None	No	High	$0.25N_0$
16	Baldchin Groper	None	No	High	$0.50N_0$
17	Dhufish	None	No	Low	$0.25N_0$
18	Dhufish	None	No	Low	$0.50N_0$
19	Dhufish	None	No	High	$0.25N_0$
20	Dhufish	None	No	High	$0.50N_0$
21	Dhufish	None	Yes **	Low	$0.25N_0$
22	Dhufish	None	Yes **	Low	$0.50N_0$
23	Dhufish	None	Yes **	High	$0.25N_0$
24	Dhufish	None	Yes **	High	$0.50N_0$

[8] Refer to Supplementary Data for further details.

Table 2. Fixed constants used in simulations. N/A = not applicable, ** = not reported here[9], - = not done.

Parameter	Snapper	Baldchin Groper	Dhufish	Source
Population dynamics				
"Low" growth, ↓ r	0.1	0.15	0.05	Preliminary
"High" growth, ↑ r	0.35	0.45	0.30	Preliminary
Mean fish weight, $\overline{W}$ (kg fish^{-1})	2	3	5	Anon (2010)
No. population sub-units, n_a	141	126	167	CPUE dataset
No. 60′ blocks, n_k	8	7	12	CPUE dataset
No. management areas, n_m	3	3	4	Specified value (Fig. 1)
Spatial sub-unit CV, s_a	0.047	0.177	0.059	CPUE dataset[9]
Spatial autocorrelation, λ	N/A	N/A	0.75	Specified value[9]
Spatial autocorrelation, $\sigma_{\epsilon,x,y}$	N/A	N/A	0.104	CPUE dataset[9]
Movement: Diffusion rate	0 %	0 %	0 %	Assumed: base case
	10 %**			Within the range reported in Lenanton et al. (2009).
Movement: DDHS, V: ↑ r ↑ D	500**	-	-	Tuned parameter[9]
Movement: DDHS, V: ↑ r ↓ D	1 300**	-	-	Tuned parameter[9]
Movement: DDHS, V: ↓ r ↑ D	12 000**	-	-	Tuned parameter[9]
Movement: DDHS, V: ↓ r ↓ D	18 750**	-	-	Tuned parameter[9]

[9] Refer to Supplementary Data for further details.

Parameter	Snapper	Baldchin Groper	Dhufish	Source
Fishery dynamics				
"Moderate" depletion, ↓ D	50 %	50 %	50 %	Specified value
"High" depletion, ↑ D	25 %	25 %	25 %	Specified value
Percent commercial catches, P_C	80 %	50 %	50 %	Anon (2010)
Mean commercial catch, $\bar{C}$ (kg yr^{-1})	254 000	33 600	185 000	Mean of observed catches:
				1990—2005; St John and King (2006)
Fleet size, n_V	19	19	23	CPUE dataset[9]
Multinomial size parameter, θ	16	8	8	CPUE dataset[9]
Vessel log-CPUE CV, s_v	0.111	0.424	0.141	CPUE dataset[9]
Residual error log-CPUE CV, s_ϵ	0.217	0.374	0.218	CPUE dataset[9]

Table 3. Imputation methods. y_{mis} denotes the years of missing data, with $\dot{I}_y$ denoting the imputed value for year y, for each of three different types of missing data period: Before (Years 1—10); Gap (Years 11—21); After (Years 22—30). Refer to footnotes for further details.

Method	**Formula**[10,11,12]	**Footnote(s)**
Base	$\dot{I}_y = \begin{cases} I_A & 1 \le y_{\text{mis}} \le 10 \\ \text{mean}(I_A, I_B) & 11 \le y_{\text{mis}} \le 20 \\ I_A & 21 \le y_{\text{mis}} \le 30 \end{cases}$	
Linear	$\dot{I}_y = I_A + \dot{\beta}(y - A)$	13
Geometric	$\dot{I}_y = \begin{cases} I_A e^{\left(\sqrt[(B-A)]{(y-A)\cdot\log(I_B/I_A)}\right)} & \dot{\beta} > 0 \\ I_A\left(2 - e^{\dot{\beta}_2(y-A)}\right) & \dot{\beta} < 0 \end{cases}$	14
Negative Exponential	$\dot{I}_y = \begin{cases} I_A + I_B\left(1 - e^{\left(\sqrt[(B-A)]{(y-A)\cdot\log(I_A/I_B)}\right)}\right) & \dot{\beta} > 0 \\ I_A - I_B\left(1 - e^{\left(\sqrt[(B-A)]{(y-A)\cdot\log(I_A/I_B)}\right)}\right) & \dot{\beta} < 0 \end{cases}$	
Logistic	$\dot{I}_y = \begin{cases} I_A + \phi + \dfrac{\gamma - \phi}{1 + \delta e^{-\psi(y-A)}} & \dot{\beta} > 0 \\ I_B + \gamma - \dfrac{\gamma - \phi}{1 + \delta e^{-\psi(y-A)}} & \dot{\beta} < 0 \end{cases}$	15,16,17,18

[10] I_A = value for the year (y=A) preceding or commencing a missing data period (Before: $I_A = \frac{1}{3}\sum_{y=11}^{13} I_y$; Gap: $I_A = I_{10}$; After: $I_A = I_{20}$).

[11] I_B = value for the year (y=B) following or ending a missing data period (Before: $I_B = I_{11}$; Gap: $I_B = I_{21}$; After: I_B was a value projected for Year 30).

[12] Projected I_B for After period: $I_B = I_A + \dot{\beta}_{\text{Gap}}(B - A)$. $\dot{\beta}_{\text{Gap}}$ is the calculated linear rate of change in I_y either side of an observed Gap period of missing data.

[13] $\dot{\beta} = (I_B - I_A)/(B - A)$

[14] $\dot{\beta}_2 = \frac{1}{B-A}\log\left[\frac{|\dot{\beta}|(B-A)}{I_A}+1\right]$

[15] $\gamma = |I_B - I_A|$

[16] $\phi = \begin{cases} 1 & \text{if } \gamma \ge 1 \\ 0.001 & \text{if } \gamma < 1 \end{cases}$

[17] $\delta = \frac{\gamma}{\phi} - 1$

[18] $\psi = \frac{2\log(\gamma-\phi) - 2\log\phi}{B-A}$

Table 4. Summaries for medians of average MSEs. n = number of cases (stocks × scenarios × imputation types); Neg. Exp. = Negative Exponential; $\uparrow r$ = High Growth; $\downarrow r$ = Low Growth; $\uparrow D$ = High Depletion; $\downarrow D$ = Moderate Depletion.

a) Summaries by category: Percentage of cases with lowest median[19,20].

	n	Base	Linear	Geometric	Neg. Exp.	Logistic
All	72	**40.3**	22.2	23.6	4.2	9.7
$\uparrow r$	36	11.1	30.6	**41.7**	8.3	8.3
$\downarrow r$	36	**69.4**	13.9	5.6	0.0	11.1
$\uparrow D$	36	27.8	19.4	**30.6**	8.3	13.9
$\downarrow D$	36	**52.8**	25.0	16.7	0.0	5.6
$\uparrow r \uparrow D$	18	0.0	16.7	**50.0**	16.7	16.7
$\uparrow r \downarrow D$	18	22.2	**44.4**	33.3	0.0	0.0
$\downarrow r \uparrow D$	18	**55.6**	22.2	11.1	0.0	11.1
$\downarrow r \downarrow D$	18	**83.3**	5.6	0.0	0.0	11.1

b) Methods with lowest median: No Movement Scenarios[21].

Stock	Scenario	Type		
		Before	Gap	After
Snapper				
	$\uparrow r \uparrow D$	Neg. Exp.	Geometric	Geometric
	$\uparrow r \downarrow D$	Base	Linear	Logistic
	$\downarrow r \uparrow D$	Base	Linear	Geometric
	$\downarrow r \downarrow D$	Base	Base	Logistic
Baldchin Groper				
	$\uparrow r \uparrow D$	Logistic	Linear	Geometric
	$\uparrow r \downarrow D$	Base	Linear	Geometric
	$\downarrow r \uparrow D$	Base	Linear	Geometric
	$\downarrow r \downarrow D$	Base	Base	Linear
Dhufish				
	$\uparrow r \uparrow D$	Logistic	Geometric	Geometric
	$\uparrow r \downarrow D$	Base	Base	Base
	$\downarrow r \uparrow D$	Base	Linear	Linear
	$\downarrow r \downarrow D$	Base	Base	Base

[19] Scenarios in Table 4a include Diffusion and DDHS for Snapper and Spatial Autocorrelation for Dhufish: see Supplementary Data.
[20] Highest percentages in **bold**
[21] This presentation does not reflect the size of differences between medians or that in many cases there is a large overlap in distributions of average MSE between methods, so please refer also to Fig. 3 when interpreting these results.

Figure Captions

Figure 1: Spatial distribution of simulated stocks and fishery management areas. i) Left panel: Spatial management areas for the WCDSIMF (2008—2014). Hatched area identifies depths < 250 m, within which the majority of fishing effort occurs. Overlaid boxes outline simulated stock boundaries (right panels). Dashed grey line separates simulated m_2 and m_3 management areas; otherwise northern and southern boundaries of the simulated management areas align with those for the fishery. ii) Right panels: Simulated stocks. Solid squares are $10'$ blocks identifying population sub-units. Grey squares are $10'$ blocks obtained from 2002/03 Charter fishing logbook returns in Wise et al. (2007). Grey degree lines of latitude and longitude delineate $60'$ blocks. Simulated management areas: m_1 = diagonal hatching; m_2 = white; m_3 = vertical hatching; m_4 = dots; m_5 = wave hatching.

Figure 2: Comparison of mean imputed values with population abundance for each stock and type of missing data period: High Growth, High Depletion, No Movement scenarios. Error bars are standard errors presented for means of population abundances. Grey shading covers the estimated marginal means predicted from a fitted GLM for observed combinations of $60'$ block (*k*) and years (*y*), which were used to calculate the imputed values[22]. The missing data period and imputed values are those outside of the grey shading.

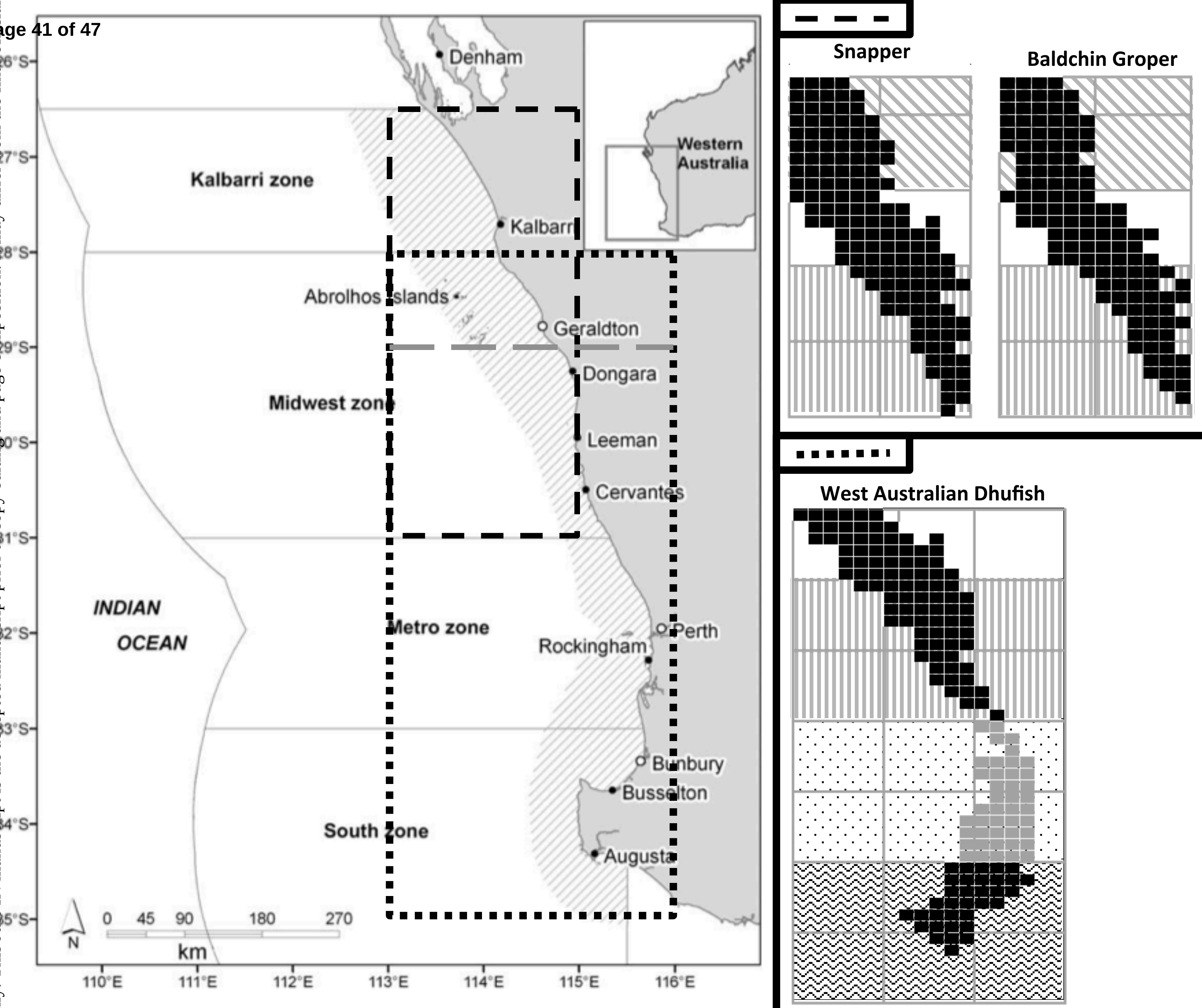
Figure 3: Box and whisker plots of average MSEs for different stocks, No Movement scenarios. Average MSE = MSE of imputed values averaged across years within each model iteration. Methods: Base (B); Linear (Li); Geometric (G); Negative

[22] Results for alternative Growth and Depletion scenarios presented in Supplementary Material.

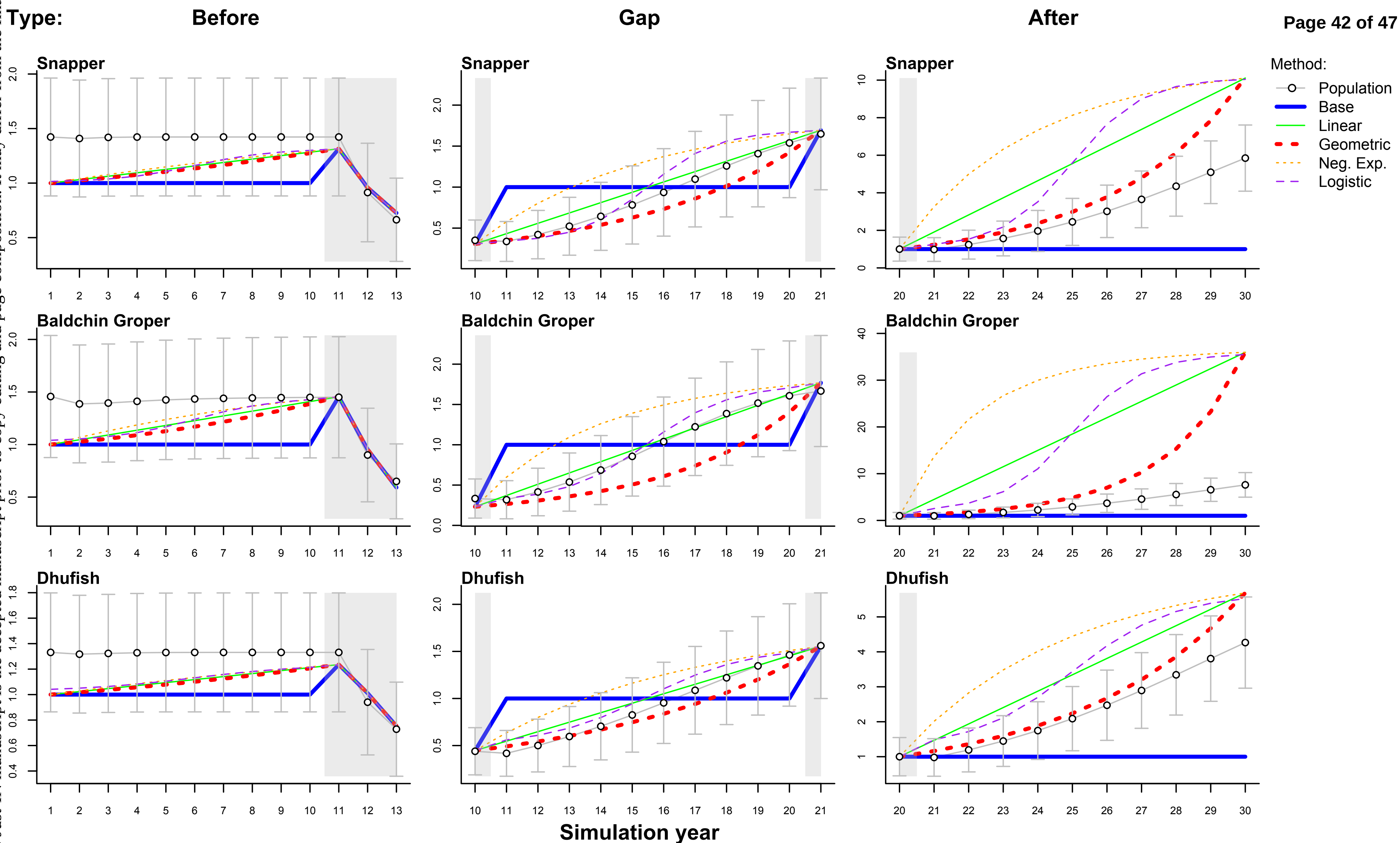
Exponential (NE); Logistic (L). Medians represented as horizontal white lines, lower and upper hinges are the first and third quartiles, whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box.

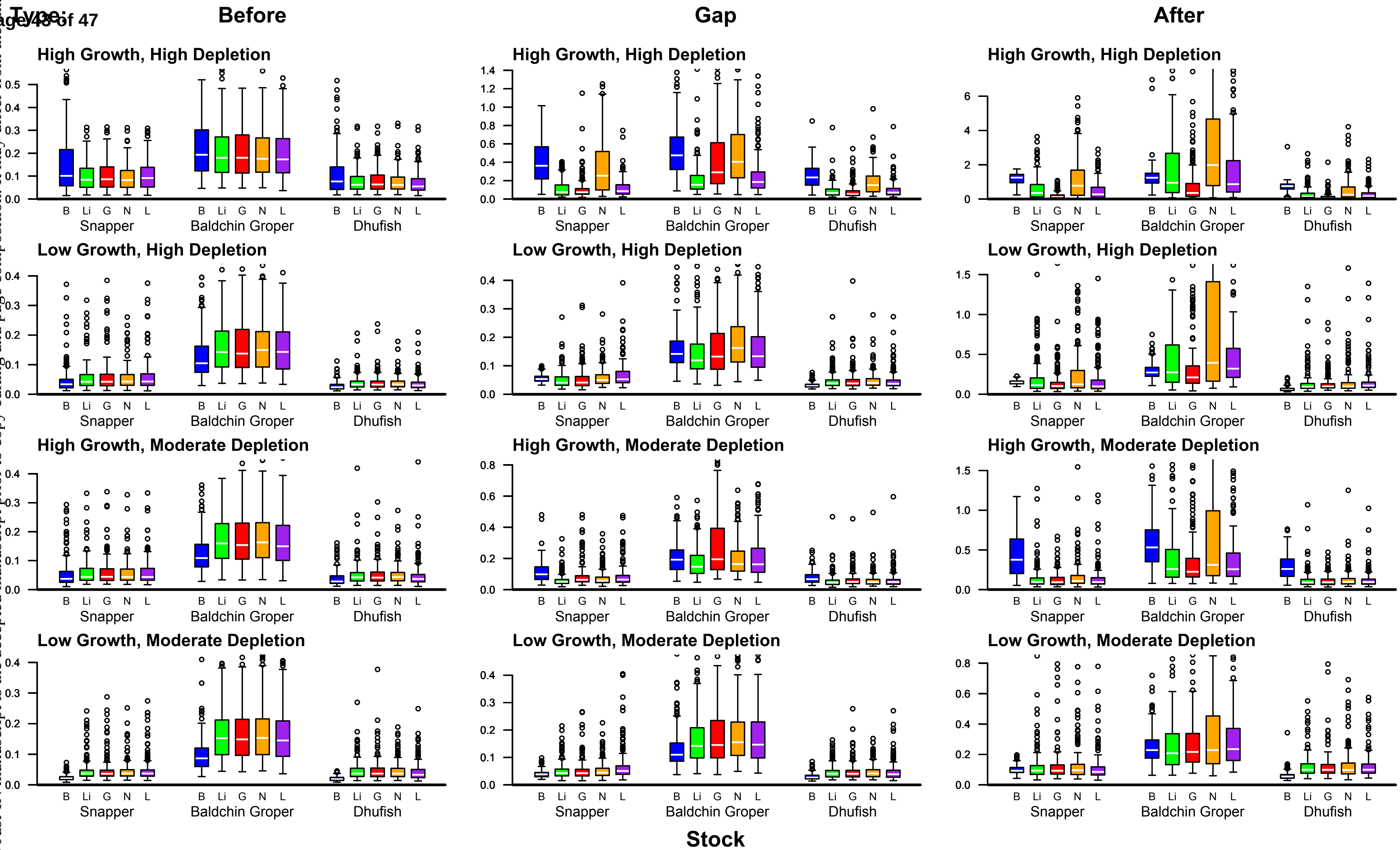
Figure 4: Mean normalised I_y and mean N_y (± standard error for population abundance and Geometric-imputed indices), High Growth, High Depletion scenario: Stocks. Error bars are standard errors for mean N_y representing stochastic variation across 200 iterations of the simulation model.

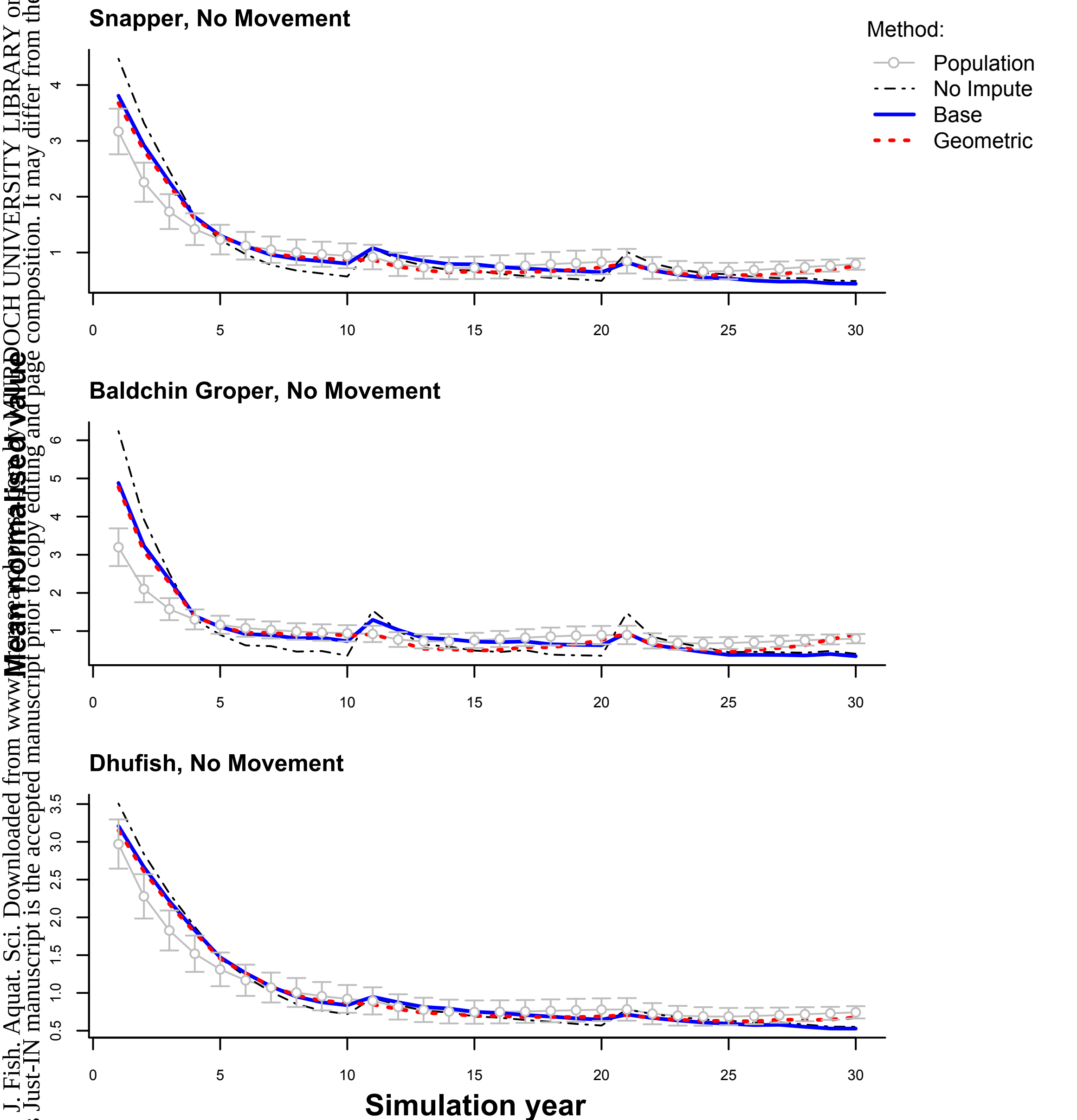
Figure 5: Mean relative error, High Growth, High Depletion scenario: Stocks. Relative error, $RE_y = \log(\text{normalised } I_y) - \log(\text{normalised } N_y)$

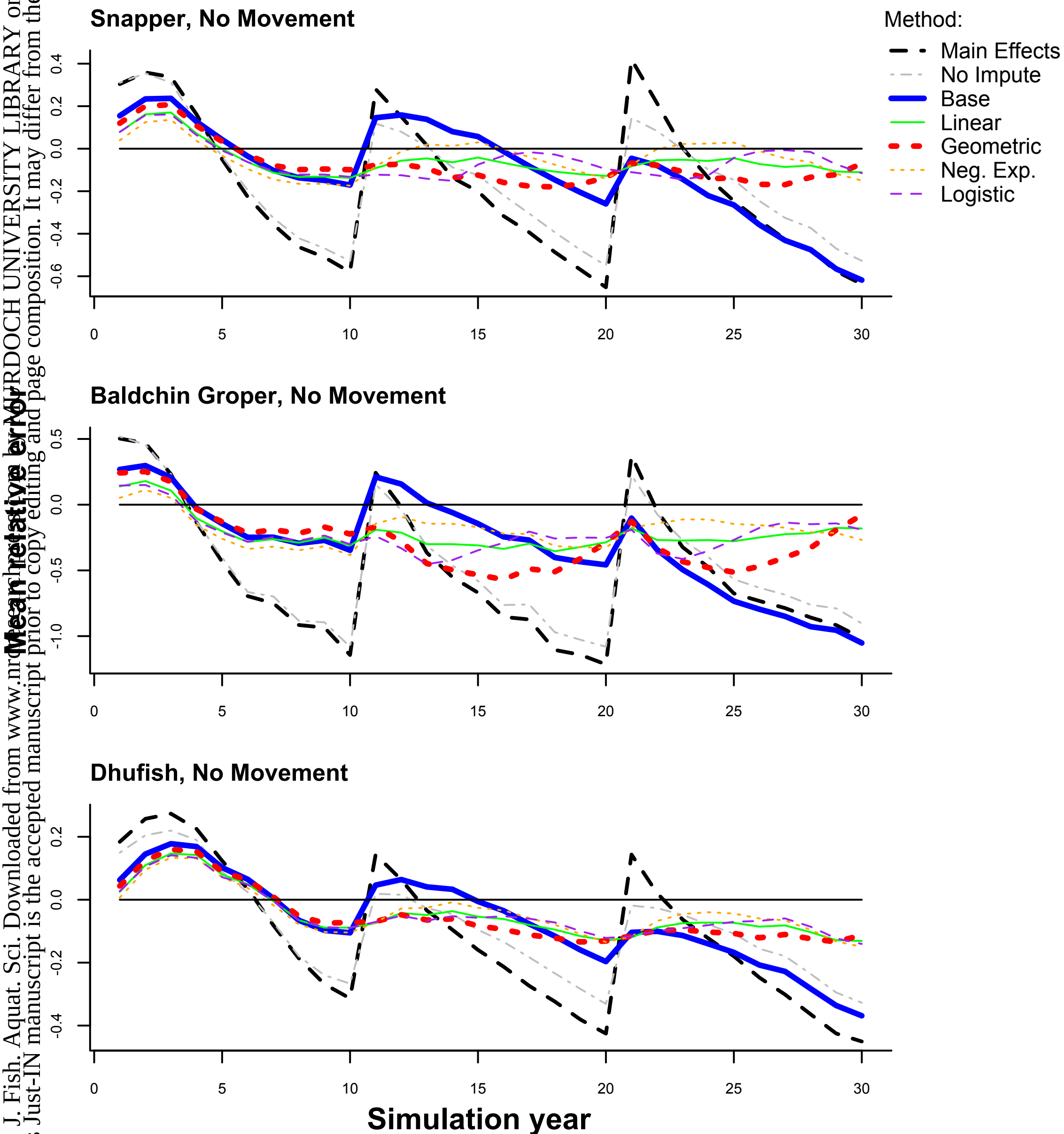


26°S
27°S
28°S
29°S
30°S
31°S
32°S
33°S
34°S
35°S
110°E
111°E
112°E
113°E
114°E
115°E
116°E
Denham
Kalbarri zone
Kalbarri
Abrolhos Islands
Geraldton
Dongara
Midwest zone
Leeman
Cervantes
INDIAN
OCEAN
Metro zone
Perth
Rockingham
Bunbury
Busselton
South zone
Augusta
0 45 90 180 270
km
N
Western
Australia
Snapper
Baldchin Groper
West Australian Dhufish


Type:
Before
Gap
After
Snapper
Baldchin Groper
Dhufish
Method:
Population
Base
Linear
Geometric
Neg. Exp.
Logistic
Mean normalised value from 200 model iterations
Simulation year


Type:
Before
Gap
After
High Growth, High Depletion
Low Growth, High Depletion
High Growth, Moderate Depletion
Low Growth, Moderate Depletion
B Li G N L
Snapper
Baldchin Groper
Dhufish
Average MSE
Stock


Snapper, No Movement
Baldchin Groper, No Movement
Dhufish, No Movement
Method:
Population
No Impute
Base
Geometric
Mean normalised value
Simulation year
0
5
10
15
20
25
30
1
2
3
4
5
6
0.5
1.0
1.5
2.0
2.5
3.0
3.5


Snapper, No Movement
Baldchin Groper, No Movement
Dhufish, No Movement
Method:
Main Effects
No Impute
Base
Linear
Geometric
Neg. Exp.
Logistic
Mean relative error
Simulation year

Appendix A. Simulation model derivation.

The model used to simulate $N_{a,y}^{\text{grow}}$ was derived from the discrete form of the logistic model for population growth, which assumed linear density-dependence in the population birth and death rates (Pianka 1974):

(A.1)

$$N_{a,y}^{\text{grow}} = N_{a,y} + rN_{a,y}\left(1 - \frac{N_{a,y}}{N_{a,0}}\right) ,$$

where *r* was the *per capita* rate of population growth:

(A.2)

$$r = b_{\max} - d_{\min}$$

with $b_{\max}$ and $d_{\min}$ representing the respective *b* and *d* at very low population sizes. The starting abundances ($N_{a,0}$) were taken as the upper asymptotic values for each respective population sub-unit and thus defined its ecological carrying capacity (Krebs 1994) at unfished equilibrium:

(A.3)

$$N_{a,0} = \frac{b_{\max} - d_{\min}}{b_{1_a} + d_{1_a}} ,$$

where b_{1_a} and d_{1_a} represent the respective rates of change in *b* and *d* with changing $N_{a,y}$.

For simplicity (and since there was no available evidence to assume otherwise), we assume symmetric rates of linear density-dependence in *b* and *d*, thus $b_{1_a} = d_{1_a}$. Hence, from Equations (A.2) and (A.3) it can be seen that b_{1_a} and d_{1_a} can be expressed in terms of $b_{\max}$, $d_{\min}$ and $N_{a,0}$:

(A.4)

$$b_{1_a} = d_{1_a} = \frac{b_{\max} - d_{\min}}{2N_{a,0}} \ ,$$

so Equation (A.1) can be reformulated as:

(A.5)

$$N_{a,y}^{\text{grow}} = N_{a,y} + N_{a,y}\left(b_{\max} - \frac{b_{\max} - d_{\min}}{2N_{a,0}}N_{a,y}\right) - N_{a,y}\left(d_{\min} + \frac{b_{\max} - d_{\min}}{2N_{a,0}}N_{a,y}\right) \ .$$

The second term in Equation (A.5) represented contributions (i.e., recruitment) due to density-dependent birth rates and the third term represented losses due to density-dependent death rates (i.e., natural mortality). Hence, replacing the $N_{a,y}$ within brackets of the second term in Equation (A.5) with $\overline{N}_{\cdot,y}$ gives us Equation (2).

References

Krebs, C. J., 1994. Ecology: the experimental analysis of distribution and abundance. HarperCollins College Publishers, New York.

Pianka, E. R., 1974. Evolutionary Ecology. CRC Press Taylor & Francis Group, New York.