Chaotic or stable? Exploring sensitivity to initial conditions of an end-to-end ecosystem model (#40962)

First submission

Guidance from your Editor

Please submit by **6 Oct 2019** for the benefit of the authors (and your $200 publishing discount).

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for general guidance.

❗ **Custom checks**
Make sure you include the custom checks shown below, in your review.

💬 **Author notes**
Have you read the author notes on the guidance page?

▦ **Raw data check**
Review the raw data. Download from the location described by the author.

🖼 **Image check**
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files
Download and review all files from the materials page.

22 Figure file(s)
3 Latex file(s)

❗ **Custom checks**

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Speculation is welcome, but should be identified as such.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Chaotic or stable? Exploring sensitivity to initial conditions of an end-to-end ecosystem model

Vidette McGregor Corresp., [1] , **Elizabeth A Fulton** [2] , **Matthew R Dunn** [3]

[1] Fisheries, National Institute of Water and Atmospheric Research Ltd
[2] Oceans & Atmosphere, CSIRO, Hobart, Tasmania, Australia
[3] Fisheries, National Institute of Water and Atmospheric Research Ltd, Wellington, New Zealand

Corresponding Author: Vidette McGregor
Email address: vidette.mcgregor@niwa.co.nz

Ecosystem models require the specification of initial conditions, and these initial conditions have some level of uncertainty. It is important to allow for uncertainty when presenting model results, because it reduces the risk of fluke or non-representative results. It is crucial that model results are presented as an envelope of what is likely, rather than presenting only one instance. We perturbed the initial conditions of the Chatham Rise Atlantis model. We found the model dynamics were not chaotic, as it generally converged, but some species groups were more sensitive to initial conditions that others. We fitted Generalised Linear Models to the sensitivity of species groups to initial conditions, offering a range of possible explanatory variables. We found trophic level explained much of the contrast, with lower trophic level species groups generally more sensitive. We recommend that in any set of scenarios explored using this model that associated uncertainty analysis include perturbations of the initial conditions, with greater changes applied to species groups that were least well informed in model development.

Chaotic or stable? Exploring sensitivity to initial conditions of an end-to-end ecosystem model

Vidette L. McGregor[1,2], Elizabeth A. Fulton[3], Matthew R. Dunn[1]

[1]Fisheries, National Institute of Water and Atmospheric Research Limited, Wellington, New Zealand
[2]School of Biological Sciences, Victoria University, Wellington, New Zealand
[3] CSIRO Oceans & Atmosphere, Hobart, Tasmania, Australia

Corresponding Author:
Vidette McGregor[1,2]

Abstract

Ecosystem models require the specification of initial conditions, and these initial conditions have some level of uncertainty. It is important to allow for uncertainty when presenting model results, because it reduces the risk of fluke or non-representative results. It is crucial that model results are presented as an envelope of what is likely, rather than presenting only one instance. We perturbed the initial conditions of the Chatham Rise Atlantis model. We found the model dynamics were not chaotic, as it generally converged, but some species groups were more sensitive to initial conditions that others. We fitted Generalised Linear Models to the sensitivity of species groups to initial conditions, offering a range of possible explanatory variables. We found trophic level explained much of the contrast, with lower trophic level species groups generally more sensitive. We recommend that in any set of scenarios explored using this model that associated uncertainty analysis include perturbations of the initial conditions, with greater changes applied to species groups that were least well informed in model development.

Keywords: Chatham Rise; Initial conditions; Chaos; Stability; Atlantis; Ecosystem model; Deep sea; Fisheries; Validation; End-to-end

1 Introduction

The Chatham Rise is perhaps New Zealand's most productive fishing ground, and fishing of many fish species and some invertebrate species began from the mid-1970s (Ministry for Primary Industries, 2017). These activities, and the notoriety of deep marine systems as sensitive or vulnerable to disturbance (Norse et al., 2012) makes the area an interesting one in terms of defining effective ecosystem based management. To assist this, an end-to-end ecosystem model has been developed—the Chatham Rise Atlantis Model (McGregor et al., 2019). One of the challenges in developing an end-to-end ecosystem model is specifying the initial conditions. In the Chatham Rise Atlantis Model (McGregor et al., 2019), the initial conditions were specified to reflect the ecosystem in it's unfished, or virgin state. We have varying levels of understanding of the components of this ecosystem in its unfished state, and as such, there are varying levels of confidence around the estimates for the initial conditions, with all components having some level of error. Hence, an important step towards understanding the dynamics and implications of this model is to explore its sensitivity to changes in the initial conditions. If we change the initial conditions slightly, does the model produce very different results - ie, is it chaotic? Or, if it is not chaotic, are some aspects of the model more stable than others?

The effects of uncertainty in the initial conditions seems to have received little attention in the development of end-to-end ecosystem models to date. In a review paper, Payne et al. (2015) found generally marine ecosystem models have not explicitly addressed uncertainty of initialisation, and more recentely, ? noted it is not something that has been done for Atlantis models. Payne et al. (2015) speculated as to the likely effects of initialisation uncertainty in end-to-end models such as Atlantis, noting long-lived species might dampen effects, and short-lived species may amplify them.

Stability, chaos, and the importance of initial conditions do, however, feature within ecological theory. There have been studies looking at what characteristics of an ecosystem are linked with stability, both from a theoretical perspective, and from observation. May (1972) showed mathematically, that large complex systems with high levels of diversity are unstable. However, there seem to be exceptions to this rule, as later studies have shown. Roberts (1974) argued that most systems in practice appear to be more stable with more connections —contrary to the mathematical analysis of May (1972). Roberts (1974) showed if only feasible solutions are included in the analyses, such that no species may have a negative population, larger systems are actually more stable. ? examined non-linear difference equations with respect to chaotic, cylclic and stable biological dynamics. Other aspects subsequently shown to increase stability of ecosystems include negative pairwise correlations (Tang and Allesina, 2014), species dispersal (Allesina and Tang, 2012), modularity (subsets of closely connected components) (Grilli et al., 2016), predator-prey relationships (Tregonning and Roberts, 1979), a high proportion of weak interactions (Olsen et al., 2016), and spatial structure (Fulton, 2001).

The Chatham Rise Atlantis model (McGregor et al., 2019) is spatially defined, although at a fairly coarse scale, using 24 dynamic polygons, and 5 water column depth layers. Species are modelled using 55 species functional groups, which include species of bacteria, detritus, phytoplankton, invertebrates, fish, sharks, cetaceans and birds. Some species groups were modelled as biomass pools, and some with age-structure, using numbers-at-age and mean weight-at-age. For many of the species, we have estimates of biomass, growth rates, age of maturity, natural mortality, spatial distributions, and diets, although some species have more knowledge gaps than others. McGregor et al. (2019) characterised the species functional groups by keystoneness, responsiveness, and informance, and these attributes may relate to stability. Keystoneness and responsiveness were quantified using model simulations perturbing a single species functional group at a time, and analysing the flow-on effects to the rest of the system. Keystoneness measures the effect changes in biomass of a species group has on the rest of the system; responsiveness measures how responsive a species group is to changes in biomass of other species groups within the system. Informance was a qualitative measure used to reflect both how well informed each species group was, and how well it performed in the model —were key dynamics such as growth, mortality rates, diets, and responses to fishing, all realistic based on what we 'know'? While these analyses were carried out to provide insight into the model's strengths and weaknesses, and highlight which gaps are likely to be most influential in model results, they are also useful for further analyses such as carried out in this study —for perturbing initial conditions in a meaningful way based on likely uncertainties, and to add further context when analysing the results.

This study goes beyond the question of whether the Chatham Rise Atlantis model is unstable, and analyses what features of the Chatham Rise ecosystem, and how we have modelled it, affect this answer. We discuss the likely impacts of our findings for future use of this ecosystem model. We highlight areas of potential future research with respect to model development, and to support decisions relating to the sustainable use of the Chatham Rise marine ecosystem resources.

2 Methods

The analyses presented here were carried out in three main sections: 1.) the initial conditions were perturbed, and the resulting model simulations were compared; 2.) components of the modelled system were characterised with respect to attributes that may affect stability; 3.) correlations between component attributes and responses to perturbations of the initial conditions were analysed, thus linking the first two sections.

2.1 Varying initial conditions

We varied the initial conditions for the number-at-age variables of age-structured species groups, and the biomass of biomass-pool species groups. For the biomass-pool species groups, biomass is the only option to perturb; Age-strurctured species groups could have errors in the specification of numbers-at-age and/or size-at-age, both of which affect the biomass-at-age. In a stock assessment model, size-at-age (or growth rates) are generally the same with respect to time, whereas there is likely a difference in numbers with respect to time (especially before fishing compared to after fishing). Hence, a different virgin biomass in a stock assessment model would generally be made up of a different number of fish, rather than the same number of fish but a different size. To align with this, we perturbed numbers rather than size for the age-strutctured species groups. The resulting number of variables to perturb was 361, of which 341 were numbers-at-age, 18 were the nitrogen content of biomass-pool species groups, and 2 were the silicate content of biomass-pool species (diatoms and microphytobenthos). The numbers-at-age of all age-classes for a given species group were scaled by the same amount for each simulation, such that the proportions-at-age were preserved, thus preserving M (instantaneous natural mortality) in the initial conditions. Our intention was to explore the model's sensitivity to its initial conditions, not uncertainty around estimated parameters. Age-structured species groups were modelled with between 2 and 10 age-classes, and were perturbed by applying one scalar for all age-classes of a given species group. This significantly reduced the number of scalars required to 57, of which 37 were for scaling numbers-at-age for age-structured species groups.

Initially, we perturbed all initial conditions using the same scalar for all variables within each model run. The scalars we used were 0.5, 0.8, 0.9, 0.95, 1.05, 1.1, 1.2, 1.5. These scalars were chosen to cover a range from slight (+/- 5%) to extreme (+/- 50%) errors in the initial conditions.

As shifting all initial conditions by the same amount may not give an indication as to how robust or sensitive the model is to mis-specification of the initial conditions where changes could vary in direction and magnitude, we next simulated multiple model runs, with the initial conditions scaled with some random variability. We scaled the initial conditions of each variable, sampling the scalar for each from a normal distribution, $N(0, \sigma)$ with σ chosen based on how large we assumed a plausible change could be.

In total, we ran three sets of simulations, and repeated each set with and without fishing.

Set 1: **All up or down**. All initial conditions were scaled (numbers for age-structured, biomass for biomass-pool) with the same scalar for each run; scalars $\in \{0.5, 0.8, 0.9, 0.95, 1.05, 1.1, 1.2, 1.5\}$

Set 2: **High uncertainty**. All initial conditions were scaled (numbers for age-structured, biomass for biomass-pool), with the scalars sampled from normal distributions with $\mu = 0$ and σ set based on the informance ratings defined in McGregor et al. (2019) (Figure 1). Biomass-pool species groups were assumed poorly specified as these were not ranked in McGregor et al. (2019), but would likely come out as poorly specified if they had been assessed more formally.

Set 3: **High keystone species**. These runs only scaled the initial conditions of species groups likely to be most influential on the system. The species groups that ranked in the top 10 for keystoneness in McGregor et al. (2019), and all biomass pool species groups were scaled using normally distributed scalars sampled with $\mu = 0$ and $\sigma = 0.25$, giving 95% confidence intervals of $\approx +/- 0.5$. All other species groups were unchanged (Figure ??).

Figure 1: *Figure separate.* Set 2 scalars used to perturb initial conditions, with scalars sampled from Normal distributions with $\mu = 0$ and $\sigma \in (0.025, 0.05, 0.1, 0.25)$ based on informance levels 1–4 respectively where 1: ‘Poorly specified’ (gold); 2: ‘Some data gaps and/or poor performance’ (magenta); 3: ‘Slight data gaps and/or poor performance’ (blue); 4: ‘No data gaps, performed well, abundance index available’ (green) (defined in McGregor et al. (2019)).

Figure 2: *Figure separate.* Set 1 scalars used to perturb initial conditions for high keystone and biomass-pool species groups, with scalars sampled from the Normal distribution with $\mu = 0$ and $\sigma = 0.25$.

2.2 Characterising the system and its components

We calculated a subset of the ecosystem indicators analysed for the base model in ? (Table 1) at each timestep for all model simulations. Mean trophic level, diversity and the ratio of pelagic to total biomass were chosen as they responded to fishing scenarios for the Chatham Rise Atlantis model (?), but didn't require catch for the calculation (so we could apply them to model runs here with or without fishing included). We analysed the results for consistencies or discrepancies in shifts of the ecosystem reflected through these indicators, with particular focus on the response of the system when heavy fishing became established during the mid-1970s.

Table 1: Key ecosystem indicators evaluated for responses to perturbing the initial conditions.

Indicator	**References**
Mean trophic level	Pauly and Watson (2005); Shin et al. (2018)
Diversity (modified Kempton's Q)	Ainsworth and Pitcher (2006)
Biomass of pelagic fishes/biomass total	Link (2005)

If certain species groups appear to be more stable than others, we wanted to be in a position to investigate whether the more stable species groups have shared characteristics —for example, are there links between sensitivities to changes in the initial conditions and how connected each species group is in the system, how abundant they are, or how long they live, or some combination of these.

To do this, we characterised species groups by keystoneness, trophic level, biomass, animal size, lifespan, background mortality, number of trophic connections, and proportion of most dominant ('top') prey. All but the final three of these indices were available from McGregor et al. (2019). The proportion of diet made up by most dominant prey, number of trophic connections, and the proportion of natural mortality that was made up of additional mortality were calculated for this study using R version 3.4.3.

2.2.1 Proportion of top prey

For each species group, we calculated the proportion of its diet that was made up by its top prey species group based on biomass consumed. This was to classify the extent to which each species group was eating as a specialist or generalist as they are modelled. It is possible for a predator to perform in the model as more of a specialist due to aggregation of species into groups —they could predate on several prey species that are modelled in the same species group. For each species group, we summed the prey eaten over the entire model region and all modelled years 1900–2015, then selected the largest proportion.

2.2.2 Number of trophic connections

The number of primary connections ranged from 1 through to 30, and with fairly even spread in between (Figure 8). Most species groups were almost fully connected by the third level, and all species groups had at least 43 tertiary connections, of the 55 available species groups. Many of the species groups had more than 20 secondary connections, and those with fewer secondary connections generally had fewer primary connections. The number of secondary and tertiary connections are unlikely to be informative for stability between runs as there is little contrast.

Figure 3: *Image separate.* Number of trophic level connections by species group for the Chatham Rise Atlantis model (base) 1900–2015 model outputs. A: Number of groups (frequency counts) by primary connections (green bars), secondary connections (blue bars), and tertiary connections (orange bars); B: Number of primary connections by species group (green bars), and number of secondary connections by species group (blue asterisks, and using right-hand axis).

2.2.3 Additional natural mortality

There is the option in Atlantis to apply additional natural mortality either as a quadratic term, which is density dependent, or as a linear term (Audzijonyte et al., 2017). The balance between additional natural mortality and mortality coming from dynamics within the model may affect the model's stability. Higher levels of additional mortality reduce the strength of connections in the model, with 100% additional mortality effectively resulting in parallel single species models. Additional mortality was required for some species groups in the Chatham Rise Atlantis model that did not suffer sufficient natural mortality through predation, starvation or disease in the model to match estimates of mortality from the literature. For all age-structured species groups in this model, linear rather than quadratic mortality was applied as this is a close approximation to instantaneous natural mortality (M). When M is small, as it is when applied at small time-steps, e^{-M} can be approximated by $1-x$ using the first two terms of its Taylor series expansion. Hence, if we take N_t to be the number of individuals at timestep t and $N_{t+\delta}$ to be the number at timestep $t+\delta$ where δ is small we get

$$N_{t+\delta} = N_t e^{-M_\delta} \approx N_t(1 - M_\delta) \tag{1}$$

As linear mortality, m_L, is applied at every timestep (12 hours for this model), we can use M_δ to approximate m_L. This is, however, complicated by a temperature effect which is applied to m_L in Atlantis. Additional mortality in Atlantis are assumed related to metabolic rates, and hence are temperature dependent. The temperature effect is applied as a scalar (T_{corr}) calculated as a function of the current water temperature (T) (in a given cell at a given time) relative to a base temperature, set at 15 ^{o}C (Equation 2).

$$T_{corr} = 2^{(T-15)/10} \tag{2}$$

As temperature varies spatially and temporally, so does the scaled m_L. We calculated the additional applied mortality for each species group based on their spatial distribution, m_L values, and temperature corrections, using the median, upper and lower quartile, and 95% confidence intervals for the applied additional mortality to reflect the variability of temperature spatially and temporally. These were calculated for both juveniles and adults as m_L and spatial distributions were defined separately for these life stages.

Total realised mortality rates were estimated from the model by fitting an exponential decay curve to the proportions-at-age. By running the model with no fishing, the realised mortality consisted entirely of natural mortality, including sources within the model such as predation, as well as additional mortality from m_L. We then compared the total realised natural mortality with the range of additional mortality to estimate what proportion of natural mortality was coming from dynamics within the model, and what proportion was forced. We produced a weighted average for each species group that combined the proportions for adults and juveniles, weighted by the numbers of adults and juveniles respectively.

2.3 Modelling stability

We analysed the effects of perturbing the initial conditions by fitting a GLM (Generalised Linear Model) to the coefficient of variation (CV) for the biomass of each species group across model runs. We used Atlantis model outputs following a 35-year burn-in period, to match the burn-in used in McGregor et al. (2019). Variables from characterising the species groups (Table 2) were offered as possible explanatory variables, using a step-wise selection algorithm, with each iteration selecting the variable (or pair of interaction variables) that explained the largest proportion of the null deviance. This process was repeated until the additional deviance explained was less than 10%. This cut-off value was selected to limit the number of explanatory variables selected, while retaining most of the explained null deviance. We initially explored untransformed, and log (base 10) and cubed root transformations of the response variable (CV), with all modelled using the Gaussian distribution. The analyses presented here used the cubed root transformation as we found this produced greater homogeneity of residuals with respect to the fitted values.

We could not model the biomass-pool species group CVs with respect to all attributes, as some attributes had not been analysed for biomass-pool groups (e.g. Keystone and Response), and some attributes relate to individuals, such as maximum size and instantaneous mortality. Hence, we fitted three versions of the GLM: 1.) limited the species groups included in the analyses to species with age-structure in order to consider the full list of explanatory variables; 2.) retained all species groups, but limited the explanatory variables offered; 3.) limited the species groups to biomass-pool species groups, with the limited the explanatory variables offered. Table 2 gives the full list of explanatory variables offered for biomass-pool (BP), age-structured (AS), and all-species (ALL) versions of the model. All possible paired interaction terms were also offered. PropByTopPrey was dropped from BP models as nearly half (8/17) of the biomass-pool species groups were not predators, and this variable only applies to predators.

We fitted the GLM to model outputs for each year (1900–2015) to test for temporal shifts in the effects (a separate GLM was fitted at each year). To allow for influence from the method of perturbing the initial conditions (all up or down, based on keystoneness, or based on uncertainty), we included this (‘ChaosAlt’) as a potential explanatory variable. We also explored splitting out the fished model runs from the unfished, or including this within ChaosAlt (Table 3).

We fitted a summary GLM for each version (ALL, AS, BP species; with/without fishing included), using a subset of the years simulated by the models, where the explanatory variables selected for models fitted at each timestep were roughly consistent. We used these summary models to explore the effects of the selected explanatory variables on between-run CVs. We analysed the residuals to check for trends or biases in the model fits, and present these as well as the effects of selected explanatory variables.

Table 2: Explanatory variables offered to explain effects of perturbing the initial conditions, and whether these were defined for age-structured species groups or biomass-pool species groups, or all species groups. BP= biomass-pool species groups; ALL= all species groups; AS = age-structured species groups.

Variable	**Model BP**	**Model ALL**	**Model AS**
1. Informance			✓
2. TL	✓	✓	✓
3. Keystone			✓
4. Response			✓
5. NumL1cons	✓	✓	✓
6. Lifespan	✓	✓	✓
7. propAdM			✓
8. propJuvM			✓
9. B0	✓	✓	✓
10. PropByTopPrey		✓	✓
11. Linf			✓
12. ChaosAlt	✓	✓	✓

Table 3: ChaosAlt definitions for perturbing the initial conditions, and including fishing in the model or not. ChaosAlt was offered as an explanatory variable to the GLMs.

ChaosAlt	**Description**	**Included fishing**
A	All up or down	
B	All up or down	✓
C	Based on uncertainty	
D	Based on uncertainty	✓
E	Based on keystoneness	
F	Based on keystoneness	✓

3 Results

3.1 Variability from initial conditions

Some species groups diverged while others converged, with biomass-pool groups more likely to have persistent high CVs between model runs (Figure 4). Fishing sometimes reduced the between-model CVs for age-structured species groups, such as for hoki, but the effects of fishing were not apparent in any biomass-pool species groups—in biomass trajectories or CVs between model runs (Figure 5 for two examples; Appendix A for the full set of figures.). Responses of age-structured species groups to fishing were generally consistent across model runs. This included direct effects of fishing on a species (such as hoki, hake, orange roughy and ling), and predation-release responses (such as cephalopods and pelagic fish). Exceptions were invert comm herb (primarily paua and kina), invert comm scav (primarily scampi), dem fish pisc (primarily giant stargazer), and seaperch, which all gave varied responses with fishing included in the model.

Figure 4: *Figure separate.* Median (solid lines), and upper and lower quartiles (dot-dashed lines) for CVs of age-structured species groups (A) and biomass-pool species groups (B) from fished model runs (blue) and unfished model runs (orange).

Figure 5: *Figure separate.*Biomass trajectories from models with fishing included (blue lines) and no fishing (orange lines) for Ref Det (refractory detritus) (A) and hoki (B), with CVs from across the model runs by time from fished models (aqua asterisks) and unfished models (cerise asterisks) overlaid and using the right-hand axis.

3.2 Characterisation

3.2.1 Ecological indicators

Ecological indicators demonstrated variability from the perturbed initial conditions that generally neither converged nor diverged throughout the model simulations. However, the responses to heavy fishing from the mid-1970's were consistent across runs, with a decline in mean trophic level, a slight increase in diversity, and an increase in the ratio of pelagic biomass over total biomass (Figure 6). There was a slight decline in mean trophic level from 1900–2015 in some of the unfished models, although the decline was approximately 0.02 of a trophic level over 100 years, so rather small.

Figure 6: *Figure separate.*Ecological indicators, mean trophic level of age-structured species groups (A), Kempton's Q (B), and biomass ratio of pelagic fishes/all age-structured species groups (C) calculated from model simulations with fishing included (blue lines), and no fishing included (orange lines) from model years 1865–2015, which includes the burn-in period of 1865–1900.

3.2.2 Proportion of top prey

Some diets consisted almost entirely of one species group, but many others did not have a dominant species with the 'top' prey making up less than 50% of the diet, and there was quite an even spread in between, with top prey making up around 50–70% of many diets (Figure 7). Not all species groups predate, which is why some species groups (such as sediment bacteria, macroalgae) do not have a highest proportion of prey.

Figure 7: *Figure separate.* Proportion of diet made up by top prey from the Chatham Rise Atlantis model (base) 1900–2015 model outputs.

3.2.3 Number of trophic connections

The number of primary connections ranged from 1 through to 30, and with fairly even spread in between (Figure 8). Most species groups were almost fully connected by the third level, and all species groups had at least 43 tertiary connections, of the 55 available species groups. Many of the species groups had more than 20 secondary connections, and those with fewer secondary connections generally had fewer primary connections. The number of secondary and tertiary connections are unlikely to be informative for stability between runs as there is little contrast.

Figure 8: *Figure separate.* Number of trophic level connections by species group for the Chatham Rise Atlantis model (base) 1900–2015 model outputs. A: Number of groups (frequency counts) by primary connections (green bars), secondary connections (blue bars), and tertiary connections (orange bars); B: Number of primary connections by species group (green bars), and number of secondary connections by species group (blue asterisks, and using right-hand axis).

3.3 Additional natural mortality

The proportion of natural mortality forced with additional mortality through the mL term ranged from just over 0.8 for spiny dogfish down to zero for several species (Figure 9). While baleen whales, cetacean other, pinnipeds and seabirds all have zero additional mortality through mL, this does not mean their populations are entirely constrained due to mortality within the model, as these groups all migrate out of the model and their populations are restrained on re-entry into the model domain. Pelagic fish small (primarily myctophids), arrow squid, cephalopods other, and invert comm scav (primarily scampi) have all their natural mortality from sources such as predation within the model. Just over half (19/37) of the age-structured species groups had more than 80% of natural mortality forced as adults. Most age-structured species groups (31/37) had less than 50% of natural mortality forced for juveniles.

Figure 9: *Figure separate.* Proportion of natural mortality (M) forced as additional mortality by species group from the Chatham Rise Atlantis model (base) 1900–2015 model outputs.

3.4 Modelling stability

3.4.1 GLMs fitted at each timestep

The models fitted at each timestep (year) with all species groups combined (ALL) selected the interaction term ChaosAlt (the way in which the initial conditions were perturbed) and trophic level, and explained just under 50% of the null deviance (Figure 10). The ChaosAlt:trophic level interaction term was also the most important explanatory variable for biomass-pool (BP) only species group models (Figure 11), and age-structured (AS) only species group models (Figure 12). BP models consistently selected a second term; the interaction of the number of primary trophic connections and virgin biomass (B_0) and explained between 50% and 60% of the null deviance (Figure 11). The AS models had different explanatory variables selected at different timesteps, and these were also influenced by whether fishing was included in the models. The interaction between ChaosAlt and the number of primary trophic connections was the most consistently selected second explanatory variable for AS models (Figure 12). The BP and AS models seemed to have a shift at around 1910. Explanatory variables selected prior to 1910 did not include ChaosAlt, but trophic level was important as an interaction with virgin biomass and the number of primary trophic connections for BP models, and trophic level and informance for AS models (Figures 11 and 12).

Figure 10: *Figure separate.* R^2 for GLMs fitted at each timestep to biomass CVs of all species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars coloured by explanatory variable.

Figure 11: *Figure separate.* R^2 for GLMs fitted at each timestep to biomass CVs of biomass-pool (BP) species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars coloured by explanatory variable.

Figure 12: *Figure separate.* R^2 for GLMs fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars coloured by explanatory variable.

3.4.2 Final GLMs

The GLMs fitted to all data from 1910–2015 selected similar explanatory variables to the GLMs fitted at each timestep (Table 4). The interaction term ChaosAlt:TL was selected first for all models, and was the only term selected for the ALL model (all-species, with fishing and non-fishing runs included). The BP (biomass-pool) only species model also selected the interaction term NumL1cons:B_0. The AS (age-structured) species only model selected interaction ChaosAlt:NumL1cons whether fishing was included or not, and a third term, interaction NumL1cons:Informance was selected for the unfished AS model.

The Pearson's residuals generally showed no concerning patterns against fitted values or explanatory variables for the final GLMs (Figures 13–17). One exception was the residuals with respect to B_0 for the BP model, which suggested decreasing errors with increasing B_0, and a possible outlier (Figure 14).

Table 4: Explanatory variables selected and corresponding r^2 values for GLMs fitted to ALL (all species groups) model CVs, BP (biomass-pool species groups) only model CVs, and AS (age-structured species groups) only model CVs, using model outputs from 1900–2015, with fished and unfished versions for AS. ChaosAlt=the set of runs, grouped by method for perturbing initial conditions and whether fishing was included or not; TL=trophic level; PrimCons=number of primary trophic connections; B_0=virgin biomass; Inf=informance;

Model	**ChaosAlt:TL**	**PrimCons:B_0**	**ChaosAlt:PrimCons**	**PrimCons:Inf**	**Total r^2**
ALL	0.47				0.47
BP	0.38	0.53			0.53
AS	0.32		0.44		0.44
AS (fished)	0.33		0.45		0.45
AS (unfished)	0.31		0.44	0.54	0.54

Figure 13: *Figure separate.* Pearson's residuals for models fitted at each timestep to biomass CVs of all (ALL) species groups that resulted from perturbing the initial conditions, using all model runs, plotted against fitted values (A), TL (trophic level) (B), and ChaosAlt (C).

Figure 14: *Figure separate.* Pearson's residuals for models fitted at each timestep to biomass CVs of biomass-pool (BP) species groups that resulted from perturbing the initial conditions, using all model runs, plotted against fitted values (A), TL (trophic level) (B), ChaosAlt (C), Number of primary trophic connections (D), and B_0 (virgin biomass) (E).

Figure 15: *Figure separate.* Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using all model runs, plotted against fitted values (A), TL (trophic level) (B), ChaosAlt (C), and Number of primary trophic connections (D).

Higher trophic level was found to be associated with lower biomass CVs for all models and ChaosAlts (Figure 18). CVs were generally lower for ChaosAlt 'A' and 'B', which were the model runs with all initial conditions shifted up or down and by the same scalar within each run. ChaosAlt 'C' and 'D', with initial conditions perturbed based on species

Figure 16: *Figure separate.* Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using fished model runs, plotted against fitted values (A), TL (trophic level) (B), ChaosAlt (C), and Number of primary trophic connections (D).

Figure 17: *Figure separate.* Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using unfished model runs, plotted against fitted values (A), TL (trophic level) (B), ChaosAlt (C), and Number of primary trophic connections (D), and informance (E). Informance levels 1–4 where 1: 'Poorly specified' (gold); 2: 'Some data gaps and/or poor performance' (magenta); 3: 'Slight data gaps and/or poor performance' (blue); 4: 'No data gaps, performed well, abundance index available' (green) (defined in McGregor et al. (2019)). Informance level '1' did not feature in the results as these data were dropped due to 'NA' values for other explanatory variables.

group uncertainty, generally had slightly higher CVs across trophic levels (Figure 18). This effect was also apparent in the interaction with primary connections in the AS model (Figure 19). Biomass CVs were found to decrease with increased B_0 and with increasing number of primary connections for biomass pool species group (Figure 19). The number of primary connections had the opposite effect for age-structured species groups, with more primary connections correlated with larger biomass CVs, although these CV effects were smaller (max. 11%) than for biomass pool species groups (max. 18%) (Figure 19).

Figure 18: *Figure separate.* GLM effects for interaction term ChaosAlt:TL for ALL species groups (A), BP only species groups (B), and AS only species groups (C). ChaosAlt 'A' and 'B' perturbed all initial conditions by the same scalar for each run; ChaosAlt 'C' and 'D' perturbed initial conditions by uncertainty; ChaosAlt 'E' and 'F' perturbed initial conditions by keystoneness; ChaosAlt 'A', 'C', 'E' did not include fishing; ChaosAlt 'B', 'D', 'F' included fishing. Shading indicates the additional CV expected for each value of the interaction, with the darkest shading in each plot corresponding to the Max. CV (%) given in the top-right corner of the plot.

Figure 19: *Figure separate.* GLM effects for interaction term PrimCons:B_0 for BP only species groups (A), ChaosAlt:PrimCons for AS only species groups (B). ChaosAlt ‘A’ and ‘B’ perturbed all initial conditions by the same scalar for each run; ChaosAlt ‘C’ and ‘D’ perturbed initial conditions by uncertainty; ChaosAlt ‘E’ and ‘F’ perturbed initial conditions by keystoneness; ChaosAlt ‘A’, ‘C’, ‘E’ did not include fishing; ChaosAlt ‘B’, ‘D’, ‘F’ included fishing. Shading indicates the additional CV expected for each value of the interaction, with the darkest shading in each plot corresponding to the Max. CV (%) given in the top-right corner of the plot.

4 Discussion

Analysing sensitivities to initial conditions is an important part of developing complex models (Rabier et al., 1996; Rosati et al., 1997; Payne et al., 2015; Cheung et al., 2016). If small perturbations to the initial conditions produce vastly different results, this may make interpreting results from the model challenging. Accounting for model uncertainty provides an envelope of model results, which tells us about the range of plausible outcomes rather than one possible instance. It is when the envelope is so wide that no result can be ascertained that it can be frustratingly un-useful, and it is important we are aware when this is the case. For example, if scenarios exploring reduced fishing effort improved the general state of the ecosystem in some model runs, and deteriorated it in others, with all runs equally plausible, then we would be left none the wiser. It would be misleading to present results of only a subset or even a singular model run that does not adequately reflect the range of plausible outcomes.

We found the Chatham Rise Atlantis model was not chaotic, in that we could perturb the initial conditions by small, and even quite large (up to 50%) changes, and the model produced very similar results with respect to biomass trends and ecosystem indicators. While the values of ecosystem indicators did not converge over the model time series, the response to fishing was consistent across model runs, suggesting system dynamics were consistent under perturbed initial conditions. This puts us in a position to simulate scenarios using the Chatham Rise Atlantis model, including uncertainty of the initial conditions, and obtain an envelope of results with which to analyse and understand the likely responses of the Chatham Rise ecosystem.

While the system as a whole generally agreed within the range of results produced, the biomasses of some species groups varied between model runs more than others. The dynamics of some species groups appeared hyperstable as they promptly converged, while others retained variability between the runs, and for some the variability increased. We found the species groups that were more likely to have high biomass CVs (coefficient of variations) were those of lower trophic levels. In nature, we expect to see more variability in the abundances of lower trophic level species, but most relevant field experts would likely suggest those patterns derive from variability within the environment (Dippner et al., 2000, 2001; Molinero et al., 2008), which we am not applying in this study. If we combined varying the initial conditions with bootstrapping of the oceanographic variables, as carried out in McGregor et al. (2019), we would likely see even greater variability in the lower trophic levels.

Another aspect of the trophic level effect on variability is the way in which we have modelled the species groups in the Chatham Rise Atlantis model. First, we have the difference between species modelled as biomass-pools and those modelled with age-structure. Biomass-pool representations are more dynamic as there is little/no delay structure built in—growth is pooled across its many forms (reproductive, somatic and otherwise), so can effectively occur instantaneously, unlike in age-structured groups where maturity may take years and specific events like spawning are restrained. Given biomass-pool groups are also generally lower trophic level (with naturally higher levels of productivity and turnover), the GLM fitted to CVs of all species groups could pick up trophic level as an explanatory variable that also accounts for this group structure. Within the age-structured species groups, trophic level could also be confounded with the proportion of additional mortality. The additional forced mortality would likely be a stabilising attribute, and the proportions applied were greater for the higher trophic level species, as these were the ones with less predation mortality in the system. That the stabilising aspect filters down through the trophic levels, with the lower trophic levels retaining variability, could suggest the extent to which this is a top-down controlled system.

The method used to perturb the initial conditions was found to be important in explaining the CVs. The runs based on keystoneness did not result in the highest CVs, even though these runs perturbed the initial conditions of the species groups expected to have the greatest impact on the rest of the system. While ? suggested keystone species have a stabilising effect on a system, it was more recently suggested to be more complicated than that (?). In this study, the possible stabilising effect of keystoneness could be due to additional mortality applied to some of the high keystone species, and hence exerting a stabilising effect on the system. The runs perturbed based on uncertainty produced the greatest CVs. The effects of other explanatory variables, such as higher CVs for lower trophic levels, were consistent regardless of the method used to perturb the initial conditions. Hence, the method was not influential in how the system responded, only in how strongly it responded. It is possible the latter difference would diminish with a greater number of runs simulated for each set. In future simulations, perturbing the initial conditions based on uncertainty would seem appropriate, and should encompass the variability we would expect to see from other methods of perturbation.

One of the age-structured species groups that was most sensitive to initial conditions was the invert comm scav group (primarily scampi). When we account for uncertainty from initial conditions, the response of this group to heavy fishing is inconclusive. The heavy fishing on the system from the mid-1970s (Ministry for Primary Industries, 2017), some of which was targeted on scampi (Tuck, 2016), could easily be positive or negative for scampi based on these model results, and CVs for this species group remained high at just over 20%. In the base Chatham Rise Atlantis model (McGregor et al., 2019), scampi were shown to respond to fishing in a very similar way to the fisheries stock assessment estimated biomass. The results here illustrate that the base model result for this species group, while convincing as it matched the fisheries models so well, was actually only one of many plausible results using this ecosystem model.

In the quest to provide meaningful and realistic results to simulations explored using complex ecosystem models, with high levels of uncertainty, we need to produce result envelopes, not single trajectories. It is important we move in the direction of simulating many instances of the model that account for its uncertainties, to understand how likely a given response is, and avoid presenting what may be fluke or non-representative results. We know there is uncertainty in defining initial conditions of ecosystem models, so varying the initial conditions to reflect this uncertainty in model results is crucial. It is not the only area of uncertainty; there are many. Given the complexity of these models, exploring all possible uncertainties explicitly is unlikely to be tractable. It may be possible, however, to address subsets of uncertainty that encompass the broader range of the uncertainty of the model by targeting its key dynamics. The key dynamics of an ecosystem model generally consist of growth, recruitment, mortality, trophic connections, environmental effects, and initial state. Three of these (growth, mortality and trophic connections) relate directly to predation and consumption, and we could vary the feeding response function to explore the effects of uncertainties in these dynamics. Initial conditions were the topic of this study, and uncertainty from environmental effects were explored through bootstrapping the oceanographic variables in McGregor et al. (2019). This leaves recruitment/productivity, for which we could vary the spawning stock recruitment parameters. The specifics of varying these will vary between models and systems, but accounting for uncertainty with respect to four main categories: 1.) initial conditions; 2.) environmental; 3.) feeding functional response; 4.) productivity/recruitment, is likely to cover the broad range for most systems and models.

5 Acknowledgements

6 References

Ainsworth, C. H., Pitcher, T. J., 2006. Modifying kempton's species diversity index for use with ecosystem simulation models. Ecological Indicators 6 (3), 623–630.

Allesina, S., Tang, S., 2012. Stability criteria for complex ecosystems. Nature 483 (7388), 205.

Audzijonyte, A., Gorton, R., Kaplan, I., Fulton, E. A., 2017. Atlantis users guide part i: General overview, physics & ecology.

Cheung, W. W., Frölicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, G., Rodgers, K. B., Rykaczewski, R. R., Sarmiento, J. L., Stock, C., et al., 2016. Building confidence in projections of the responses of living marine resources to climate change. ICES Journal of Marine Science 73 (5), 1283–1296.

Dippner, J. W., Hänninen, J., Kuosa, H., Vuorinen, I., 2001. The influence of climate variability on zooplankton abundance in the northern baltic archipelago sea (sw finland). ICES Journal of Marine Science 58 (3), 569–578.

Dippner, J. W., Kornilovs, G., Sidrevics, L., 2000. Long-term variability of mesozooplankton in the central baltic sea. Journal of Marine Systems 25 (1), 23–31.

Fulton, E. A., 2001. The effects of model structure and complexity on the behaviour and performance of marine ecosystem models. Ph.D. thesis, University of Tasmania.

Grilli, J., Rogers, T., Allesina, S., 2016. Modularity and stability in ecological communities. Nature communications 7, 12031.

Link, J. S., 2005. Translating ecosystem indicators into decision criteria. ICES Journal of Marine Science 62 (3), 569–576.

May, R. M., 1972. Will a large complex system be stable? Nature 238 (5364), 413.

McGregor, V. L., Horn, P. L., Fulton, E. A., Dunn, M. R., 2019. From data compilation to model validation: a comprehensive analysis of a full deep-sea ecosystem model of the chatham rise. PeerJ 7, e6517.

Ministry for Primary Industries, 2017. Report from the fisheries assessment plenary. stock assessments and yield estimates. Ministry of Fisheries Report.

Molinero, J. C., Ibanez, F., Souissi, S., Buecher, E., Dallot, S., Nival, P., 2008. Climate control on the long-term anomalous changes of zooplankton communities in the northwestern mediterranean. Global Change Biology 14 (1), 11–26.

Norse, E. A., Brooke, S., Cheung, W. W., Clark, M. R., Ekeland, I., Froese, R., Gjerde, K. M., Haedrich, R. L., Heppell, S. S., Morato, T., et al., 2012. Sustainability of deep-sea fisheries. Marine policy 36 (2), 307–320.

Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., Link, J. S., 2016. Ecosystem model skill assessment. yes we can! PloS one 11 (1), e0146467.

Pauly, D., Watson, R., 2005. Background and interpretation of the marine trophic indexas a measure of biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 360 (1454), 415–423.

Payne, M. R., Barange, M., Cheung, W. W., MacKenzie, B. R., Batchelder, H. P., Cormon, X., Eddy, T. D., Fernandes, J. A., Hollowed, A. B., Jones, M. C., et al., 2015. Uncertainties in projecting climate-change impacts in marine ecosystems. ICES Journal of Marine Science 73 (5), 1272–1282.

Rabier, F., Klinker, E., Courtier, P., Hollingsworth, A., 1996. Sensitivity of forecast errors to initial conditions. Quarterly Journal of the Royal Meteorological Society 122 (529), 121–150.

Roberts, A., 1974. The stability of a feasible random ecosystem. Nature 251 (5476), 607.

Rosati, A., Miyakoda, K., Gudgel, R., 1997. The impact of ocean initial conditions on enso forecasting with a coupled model. Monthly weather review 125 (5), 754–772.

Shin, Y.-J., Houle, J. E., Akoglu, E., Blanchard, J. L., Bundy, A., Coll, M., Demarcq, H., Fu, C., Fulton, E. A., Heymans, J. J., et al., 2018. The specificity of marine ecological indicators to fishing in the face of environmental change: A multi-model evaluation. Ecological Indicators 89, 317–326.

Tang, S., Allesina, S., 2014. Reactivity and stability of large ecosystems. Frontiers in Ecology and Evolution 2, 21.

Tregonning, K., Roberts, A., 1979. Complex systems which evolve towards homeostasis. Nature 281 (5732), 563.

Tuck, I., 2016. Characterisation and a length-based assessment model for scampi (*Metanephrops challengeri*) on the Mernoo Bank (SCI 3).

Appendix A: Biomass trajectories

Figure 1

Set 2 scalars used to perturb initial conditions, with scalars sampled from Normal distributions.

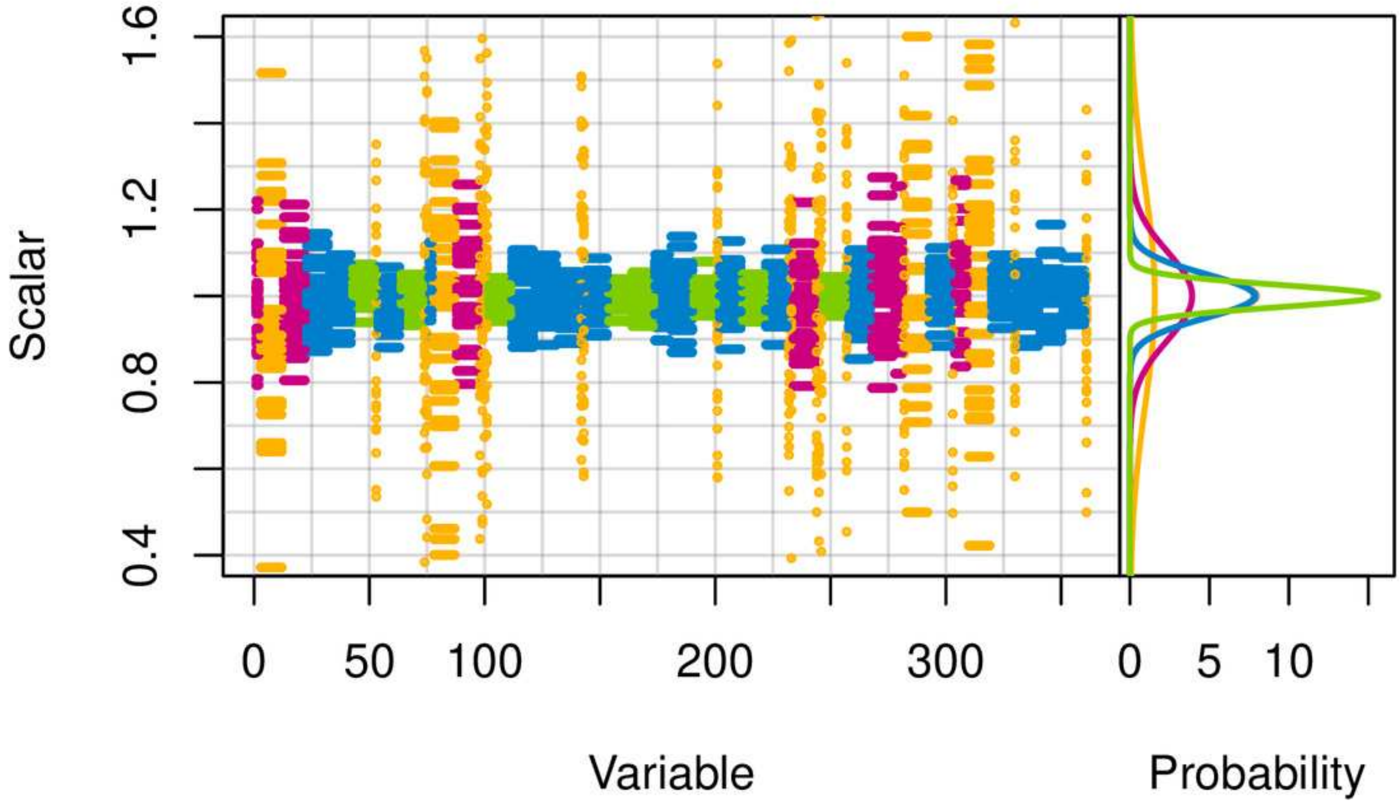


Figure 2

Set 1 scalars used to perturb initial conditions for high keystone and biomass-pool species groups, with scalars sampled from the Normal distribution.

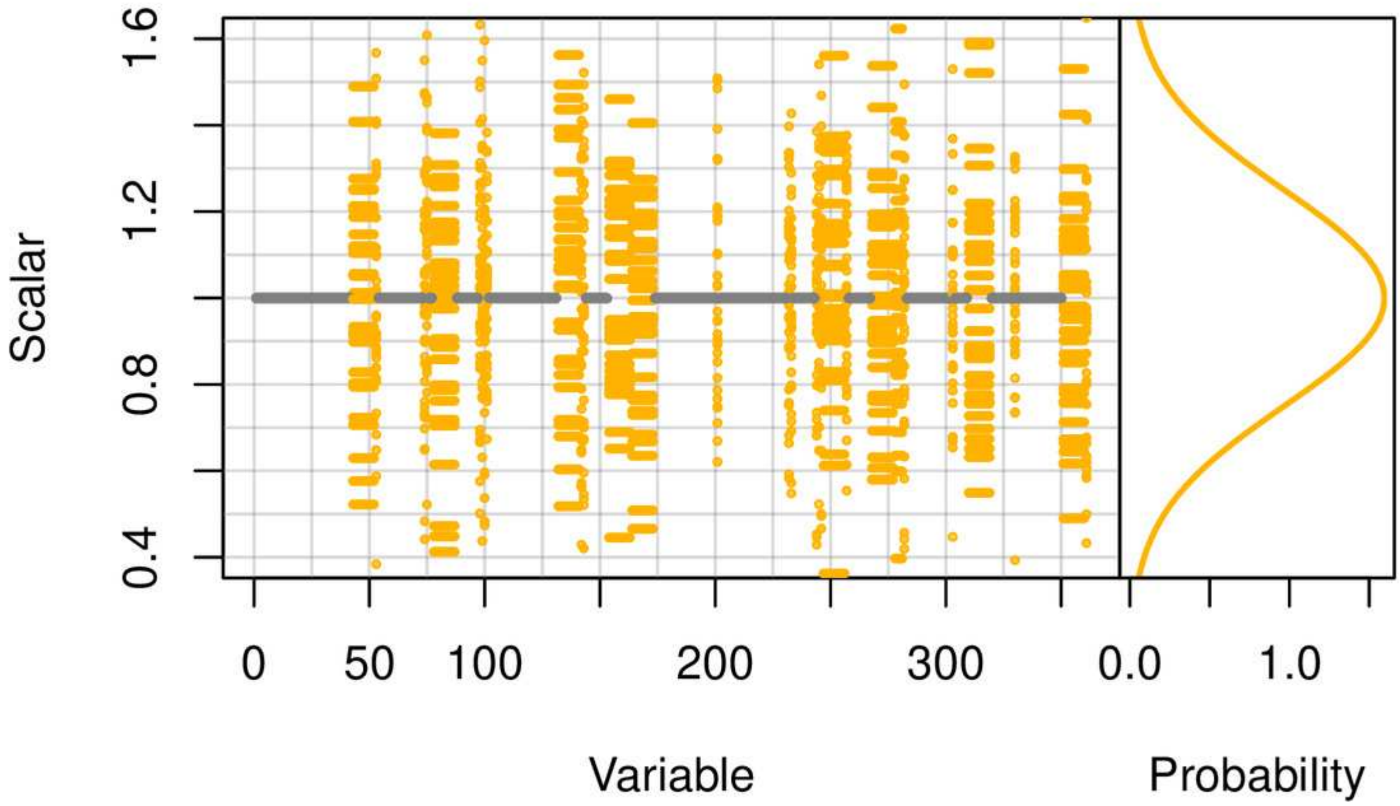


Figure 3

Number of trophic level connections by species group for the Chatham Rise Atlantis model.

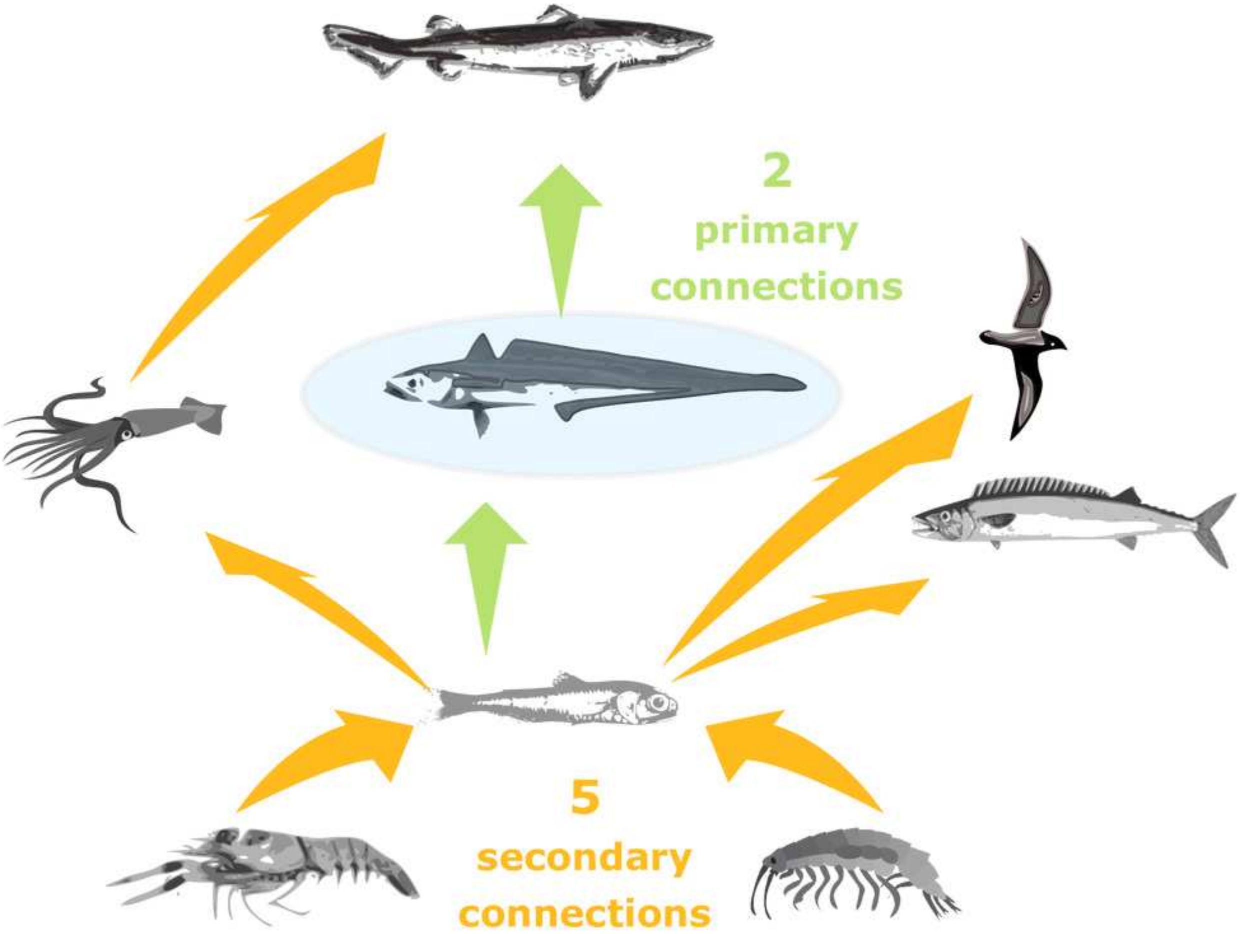


Figure 4

Median, and upper and lower quartiles for CVs of age-structured species groups and biomass-pool species groups from fished model runs and un-fished model runs.

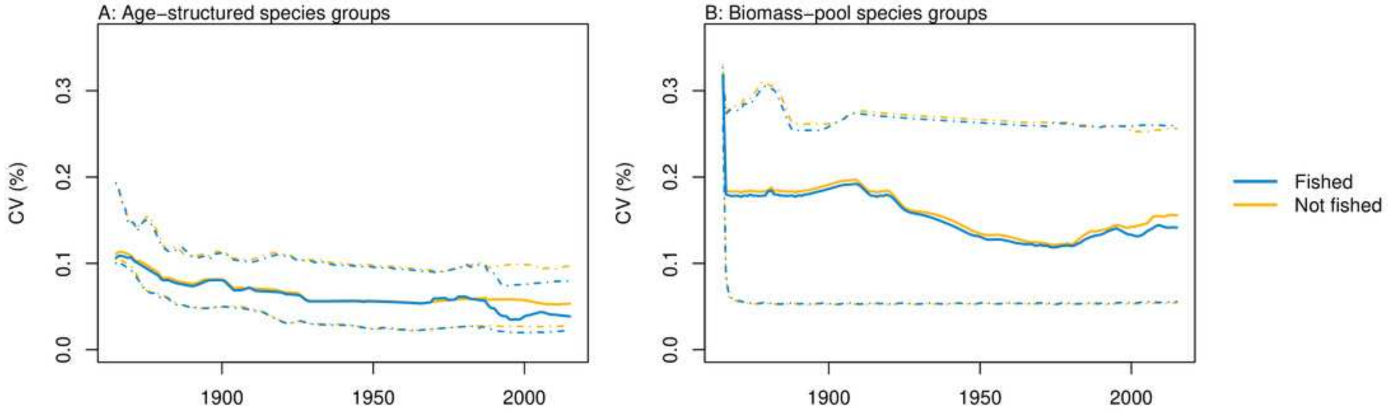


Figure 5

Biomass trajectories from models with fishing included (blue lines) and no fishing (orange lines) for Ref Det (refractory detritus) (A) and hoki (B), with CVs from across the model runs by time from fished models (aqua asterisks) and unfished models (ceri

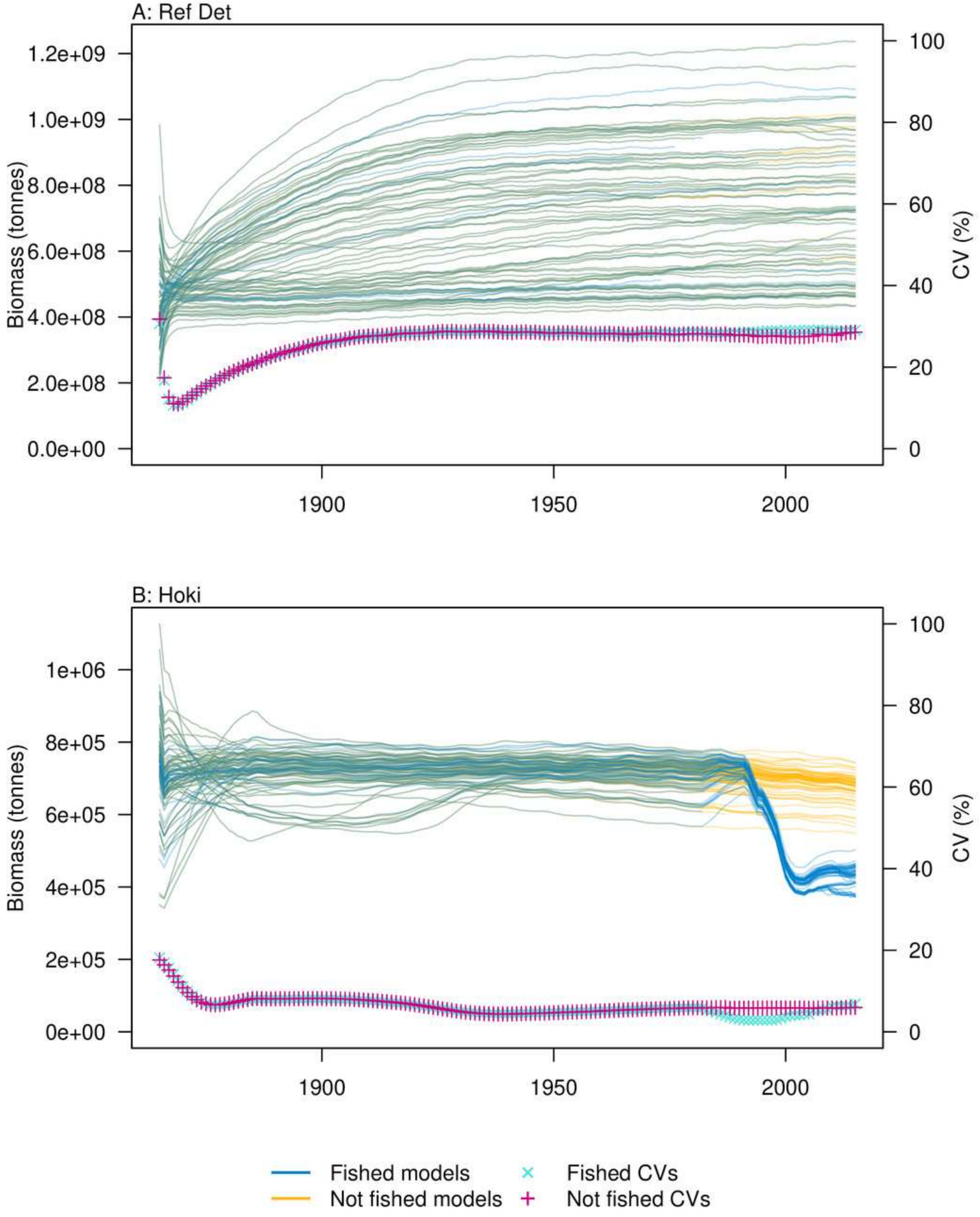

A: Ref Det
Biomass (tonnes)
1.2e+09
1.0e+09
8.0e+08
6.0e+08
4.0e+08
2.0e+08
0.0e+00
CV (%)
100
80
60
40
20
0
1900
1950
2000
B: Hoki
Biomass (tonnes)
1e+06
8e+05
6e+05
4e+05
2e+05
0e+00
CV (%)
100
80
60
40
20
0
1900
1950
2000
Fished models
Not fished models
Fished CVs
Not fished CVs

Figure 6

Ecological indicators, mean trophic level of age-structured species groups (A), Kempton's Q (B), and biomass ratio of pelagic fishes/all age-structured species groups (C) calculated from model simulations with fishing included (blue lines), and no fishing

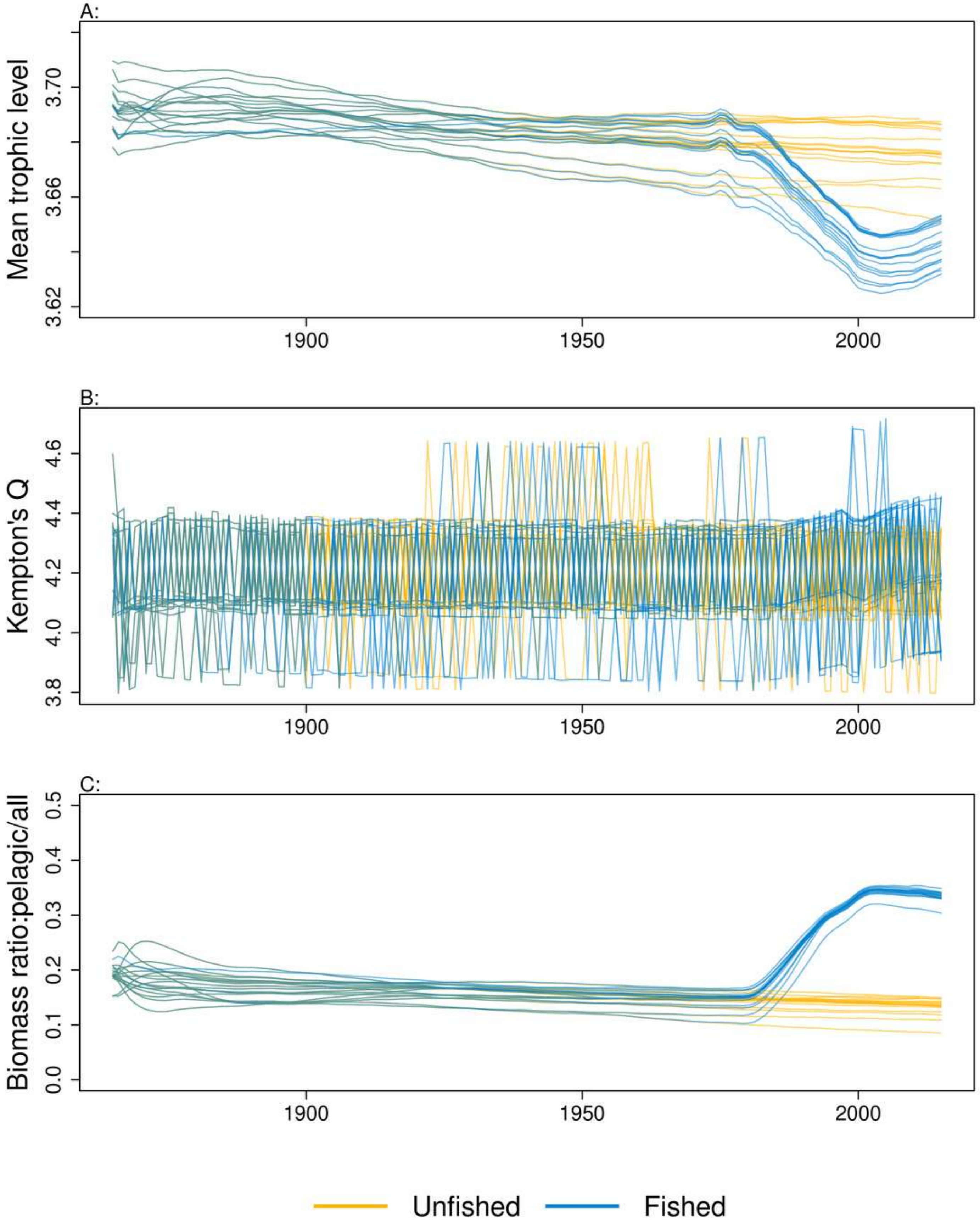

A:
Mean trophic level
3.62
3.66
3.70
1900
1950
2000
B:
Kempton's Q
3.8
4.0
4.2
4.4
4.6
1900
1950
2000
C:
Biomass ratio:pelagic/all
0.0
0.1
0.2
0.3
0.4
0.5
1900
1950
2000
Unfished
Fished

Figure 7

Proportion of diet made up by top prey from the Chatham Rise Atlantis model.

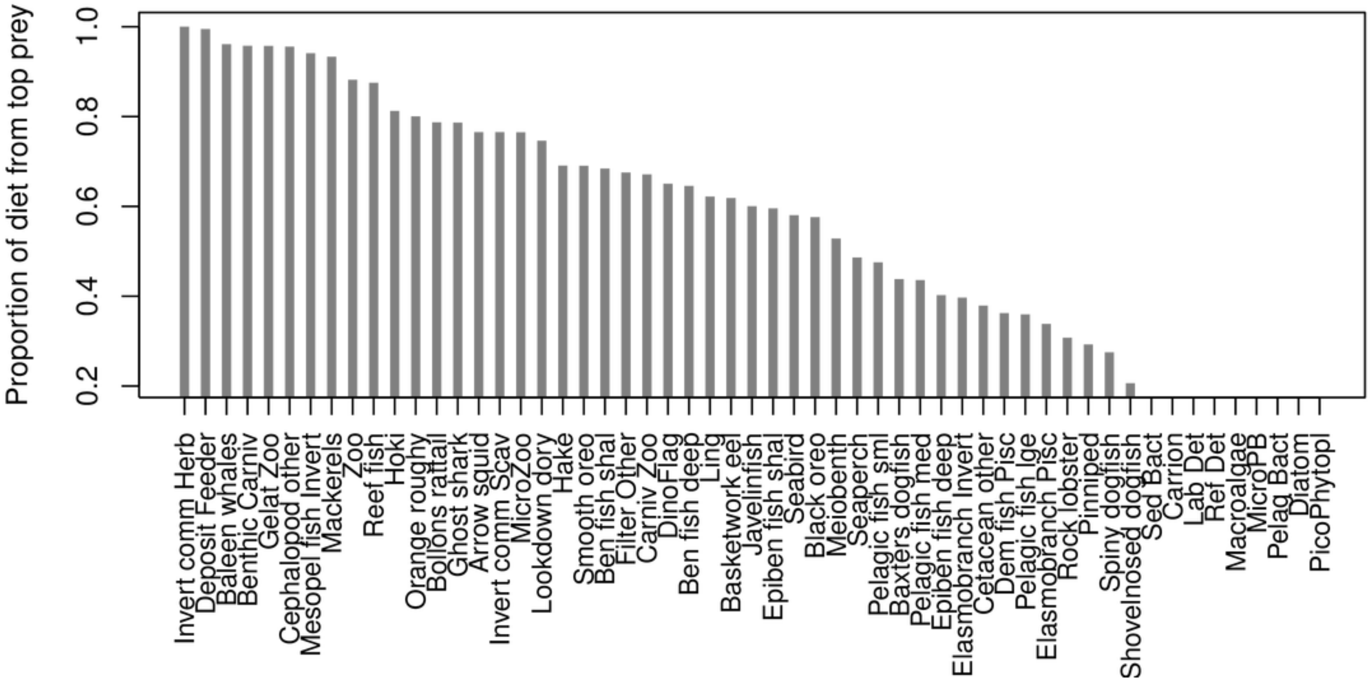


Figure 8

Number of trophic level connections by species group for the Chatham Rise Atlantis model (base) 1900\textendash 2015 model outputs. A: Number of groups (frequency counts) by primary connections (green bars), secondary connections (blue bars), and tertiary

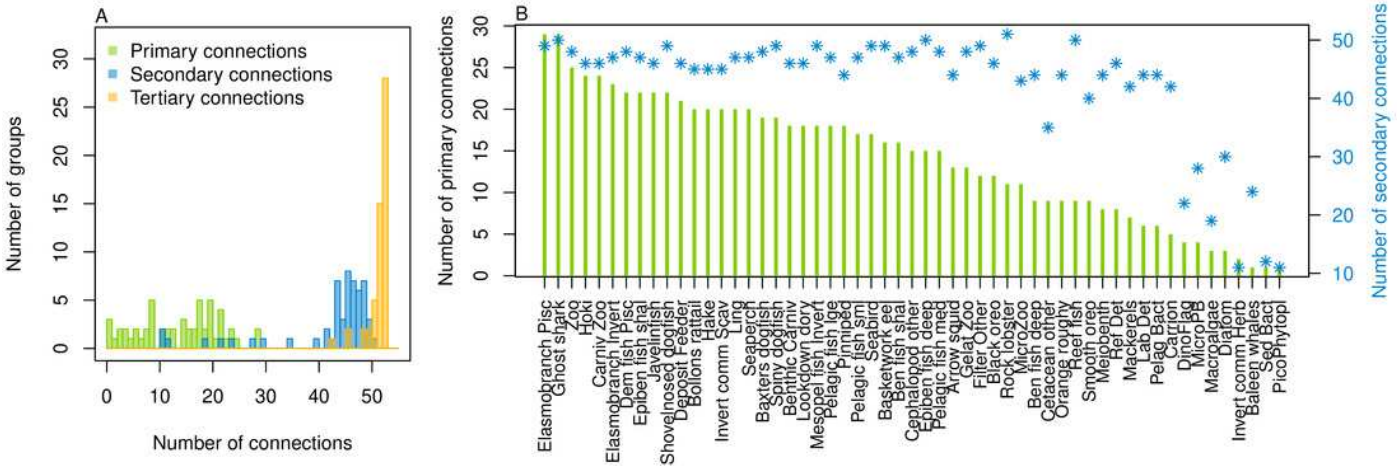


Figure 9

Proportion of natural mortality (M) forced as additional mortality by species group from the Chatham Rise Atlantis model (base) 1900\textendash 2015 model outputs.

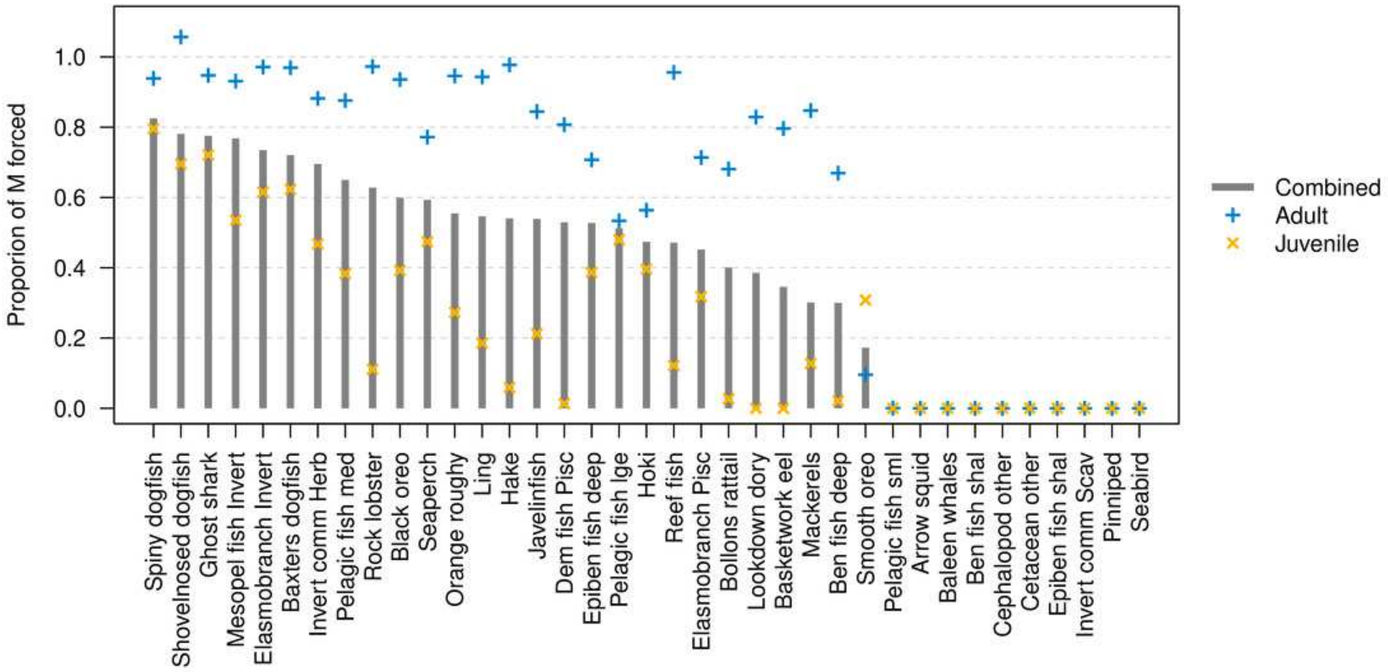


Figure 10

R^2 for GLMs fitted at each timestep to biomass CVs of all species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars coloured by explanat

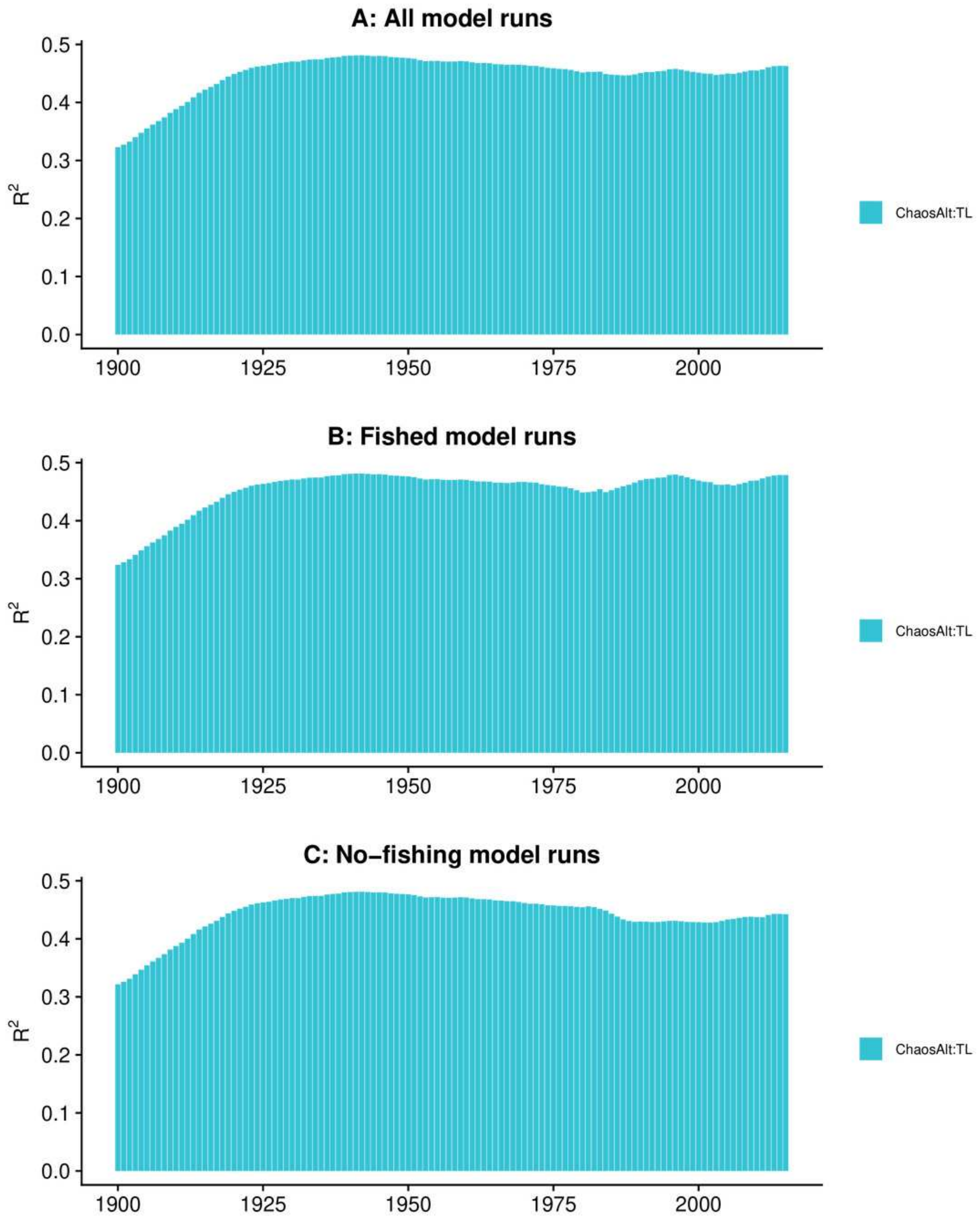

A: All model runs
B: Fished model runs
C: No−fishing model runs
R²
0.5
0.4
0.3
0.2
0.1
0.0
1900
1925
1950
1975
2000
ChaosAlt:TL

Figure 11

R^2 for GLMs fitted at each timestep to biomass CVs of biomass-pool (BP) species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars colour

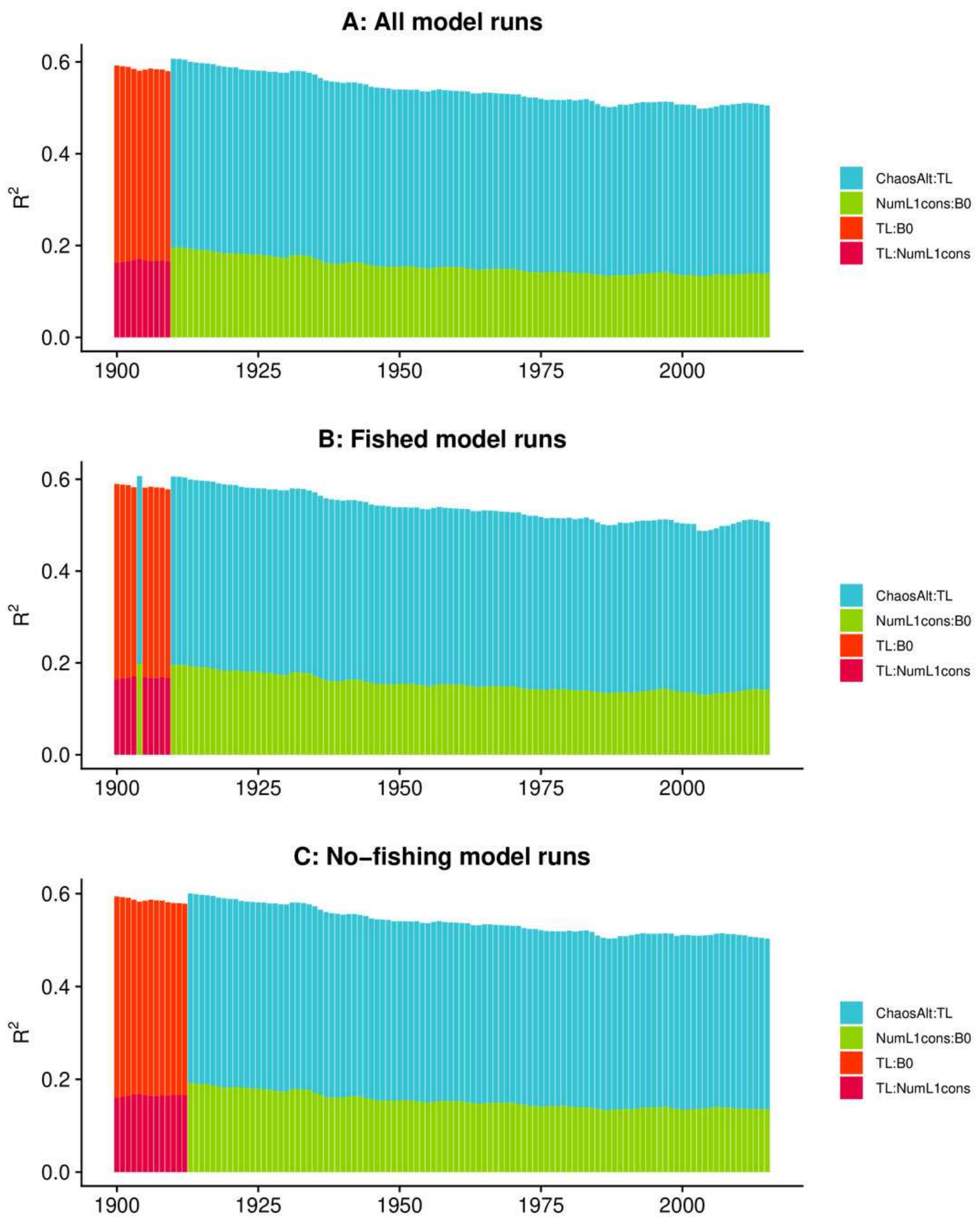

A: All model runs
B: Fished model runs
C: No−fishing model runs
R^2
0.0
0.2
0.4
0.6
1900
1925
1950
1975
2000
ChaosAlt:TL
NumL1cons:B0
TL:B0
TL:NumL1cons

Figure 12

R^2 for GLMs fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using all model runs (A), only model runs with fishing (B), and only models without fishing (C), with bars colo

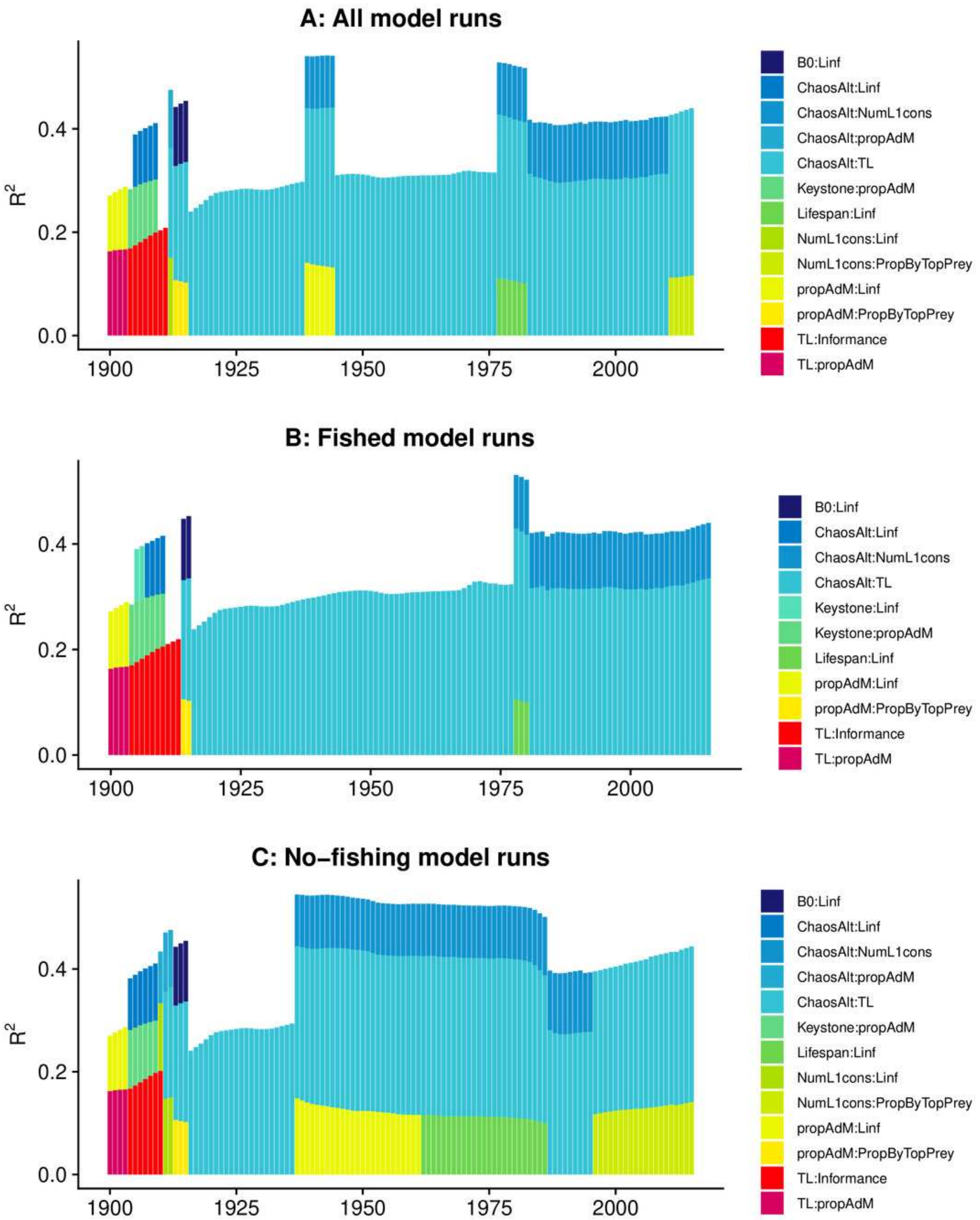

A: All model runs
R^2
0.0
0.2
0.4
1900
1925
1950
1975
2000
B0:Linf
ChaosAlt:Linf
ChaosAlt:NumL1cons
ChaosAlt:propAdM
ChaosAlt:TL
Keystone:propAdM
Lifespan:Linf
NumL1cons:Linf
NumL1cons:PropByTopPrey
propAdM:Linf
propAdM:PropByTopPrey
TL:Informance
TL:propAdM
B: Fished model runs
R^2
0.0
0.2
0.4
1900
1925
1950
1975
2000
B0:Linf
ChaosAlt:Linf
ChaosAlt:NumL1cons
ChaosAlt:TL
Keystone:Linf
Keystone:propAdM
Lifespan:Linf
propAdM:Linf
propAdM:PropByTopPrey
TL:Informance
TL:propAdM
C: No−fishing model runs
R^2
0.0
0.2
0.4
1900
1925
1950
1975
2000
B0:Linf
ChaosAlt:Linf
ChaosAlt:NumL1cons
ChaosAlt:propAdM
ChaosAlt:TL
Keystone:propAdM
Lifespan:Linf
NumL1cons:Linf
NumL1cons:PropByTopPrey
propAdM:Linf
propAdM:PropByTopPrey
TL:Informance
TL:propAdM

Figure 13

Pearson's residuals for models fitted at each timestep to biomass CVs of all (ALL) species groups that resulted from perturbing the initial conditions.

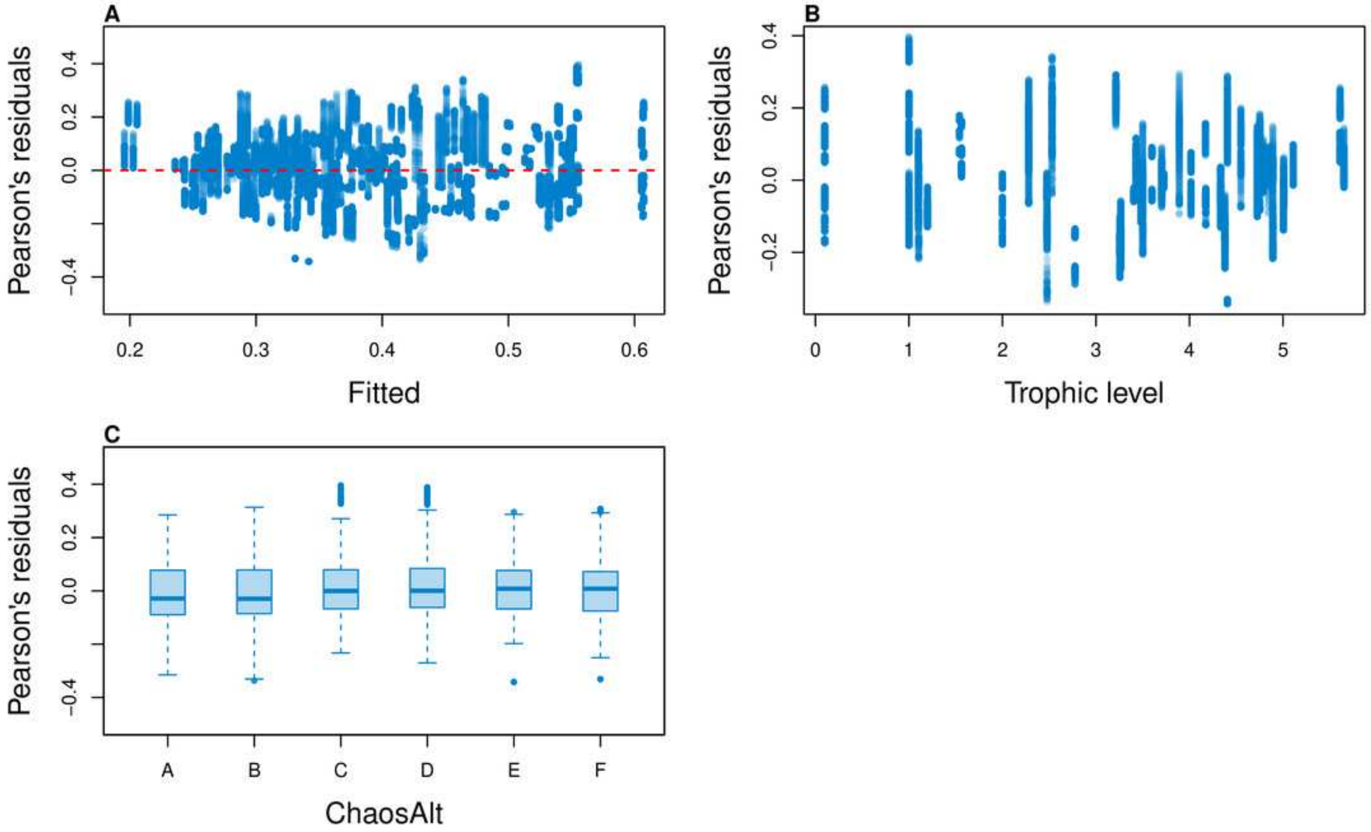


Figure 14

Pearson's residuals for models fitted at each timestep to biomass CVs of biomass-pool (BP) species groups that resulted from perturbing the initial conditions.

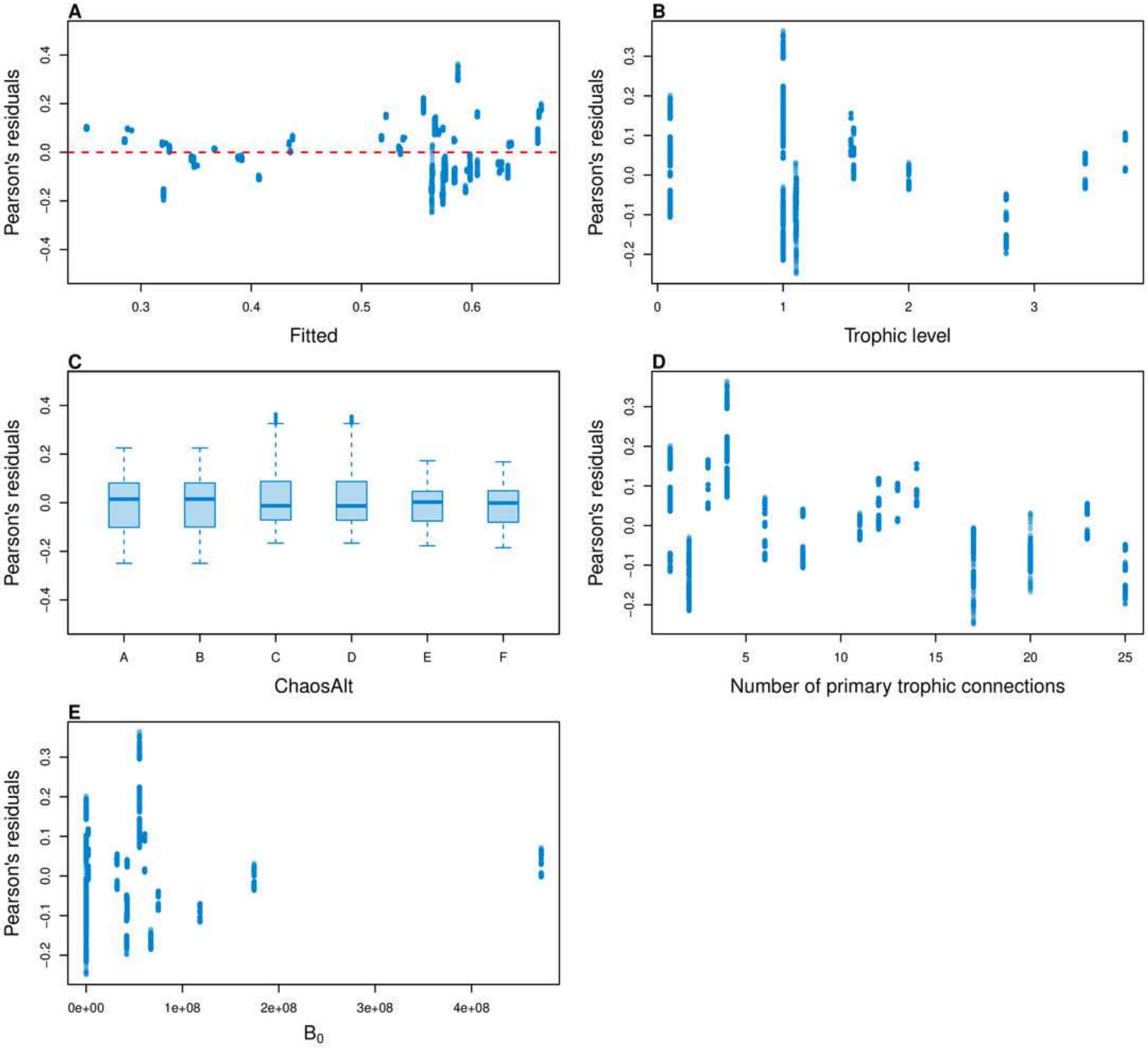


Figure 15

Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions.

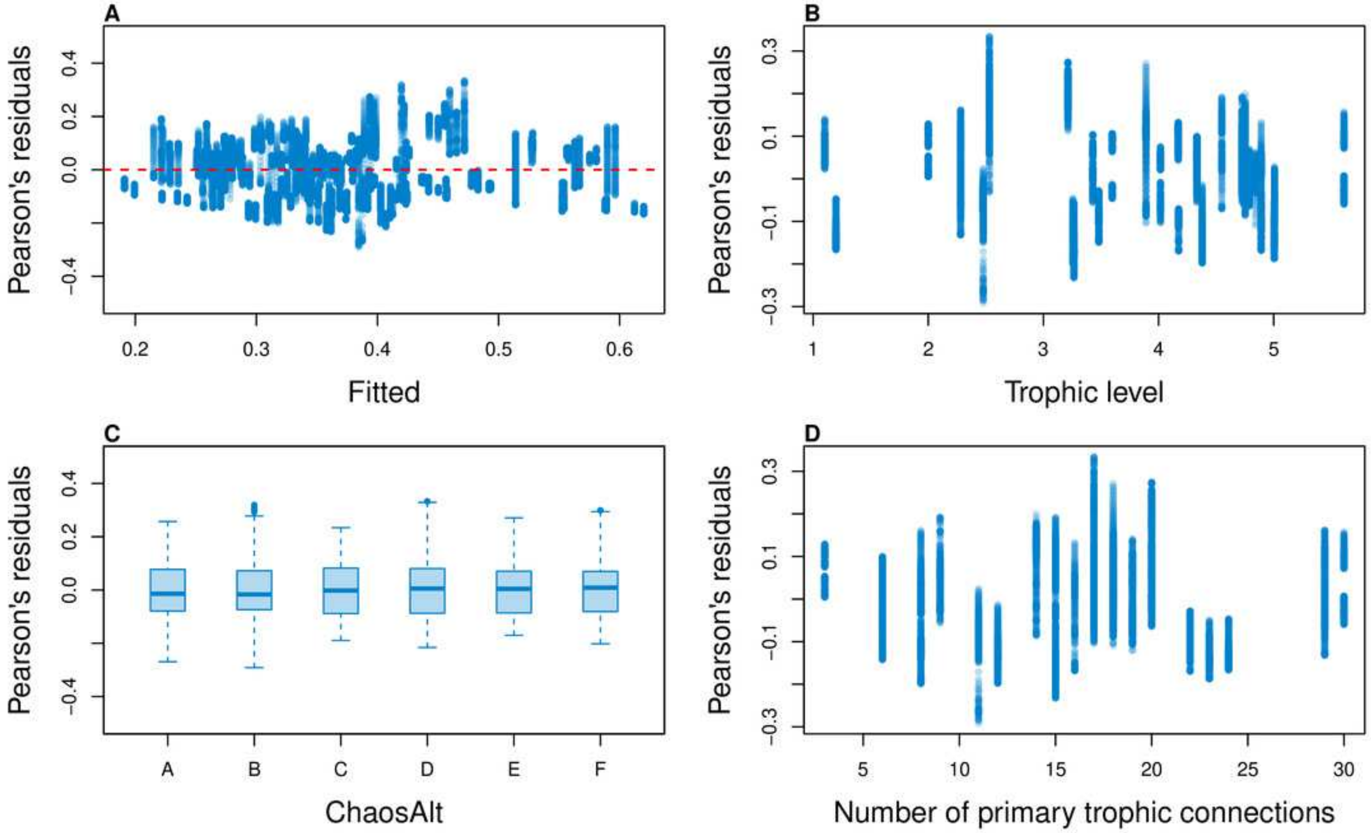


Figure 16

Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions.

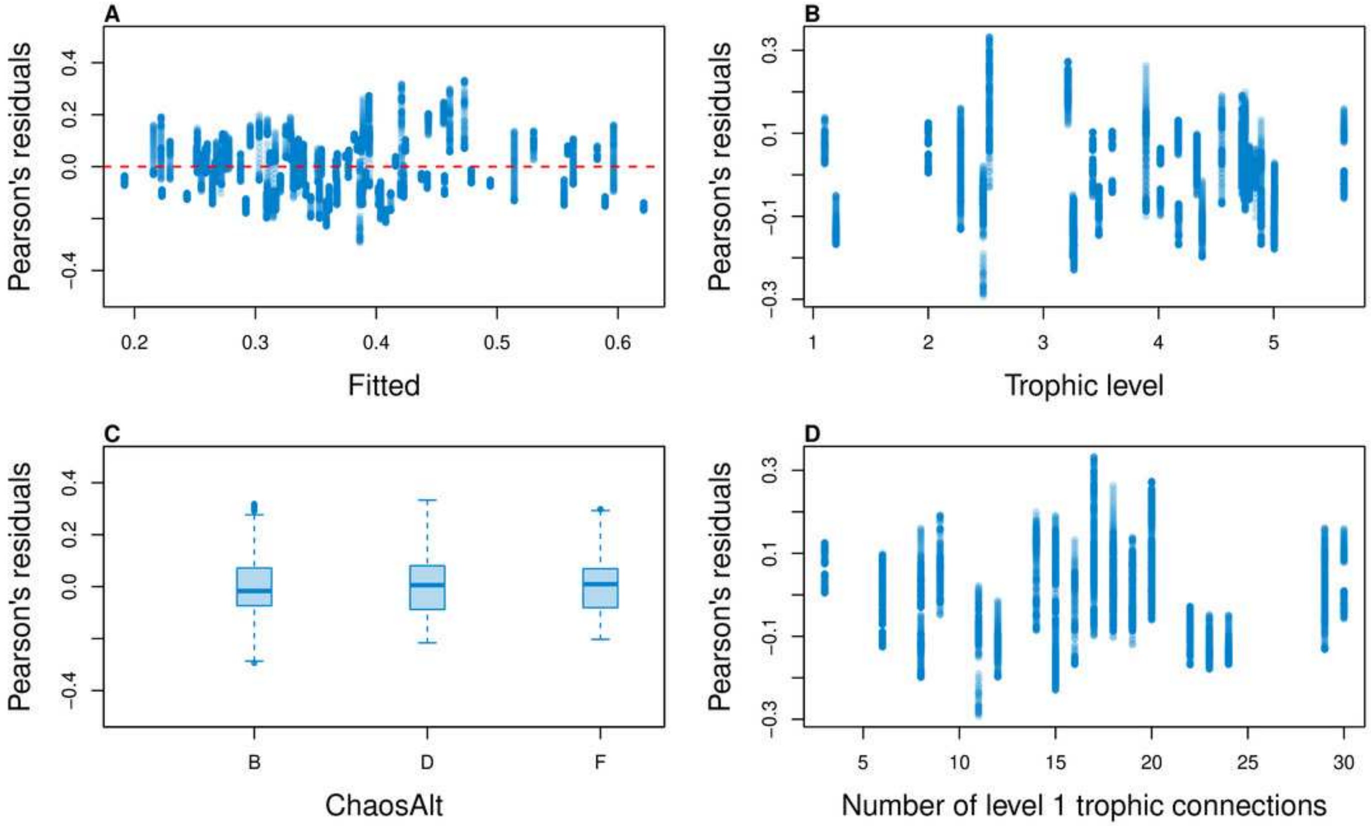


Figure 17

Pearson's residuals for models fitted at each timestep to biomass CVs of age-structured (AS) species groups that resulted from perturbing the initial conditions, using un-fished model runs, plotted against fitted values (A), TL (trophic level) (B), ChaosA

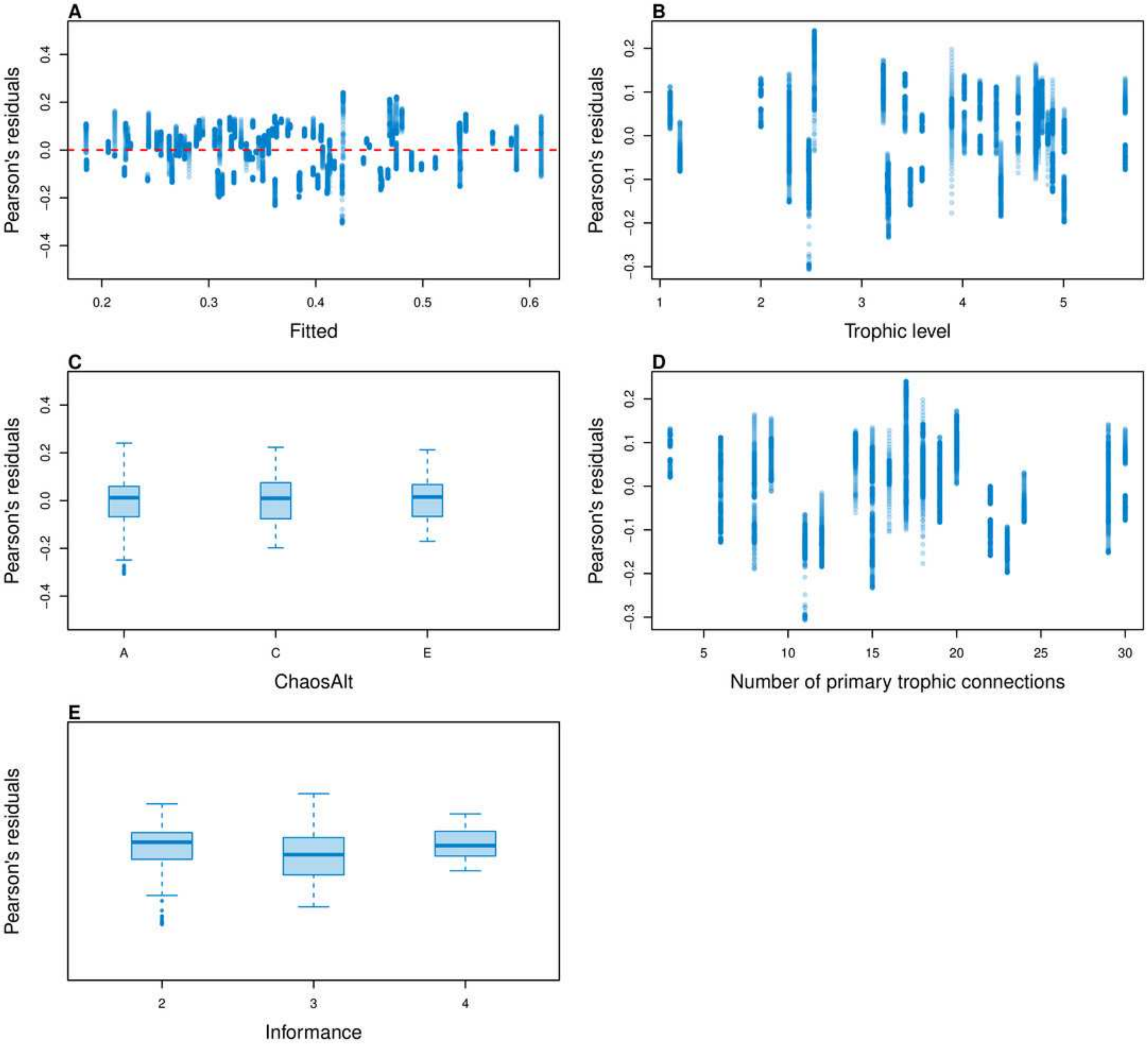


Figure 18

GLM effects for interaction term ChaosAlt:TL for ALL species groups (A), BP only species groups (B), and AS only species groups (C).

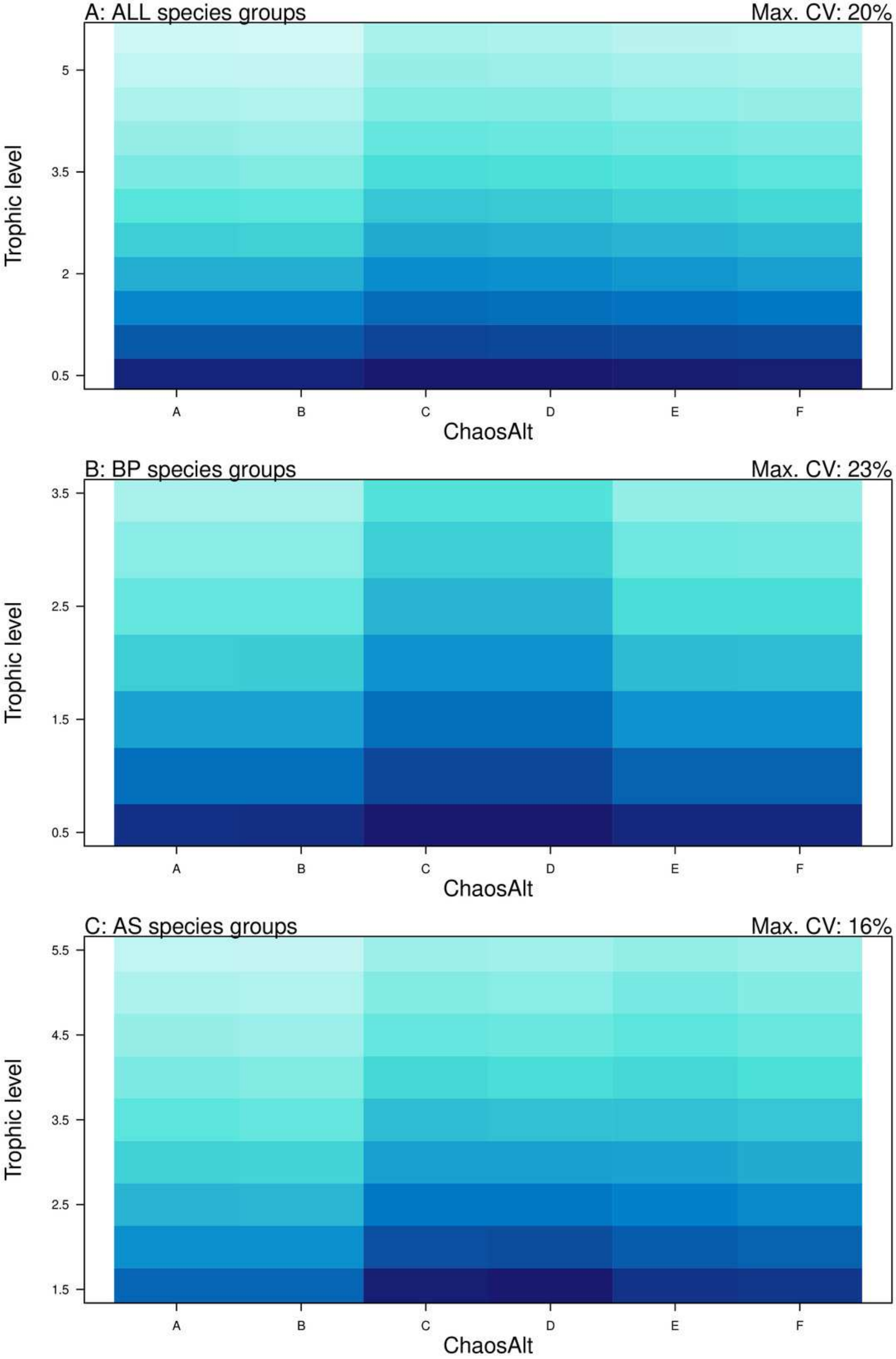

A: ALL species groups
Max. CV: 20%
Trophic level
5
3.5
2
0.5
A
B
C
D
E
F
ChaosAlt
B: BP species groups
Max. CV: 23%
Trophic level
3.5
2.5
1.5
0.5
A
B
C
D
E
F
ChaosAlt
C: AS species groups
Max. CV: 16%
Trophic level
5.5
4.5
3.5
2.5
1.5
A
B
C
D
E
F
ChaosAlt

Figure 19

GLM effects for interaction term PrimCons:B_0 for BP only species groups (A), ChaosAlt:PrimCons for AS only species groups (B).

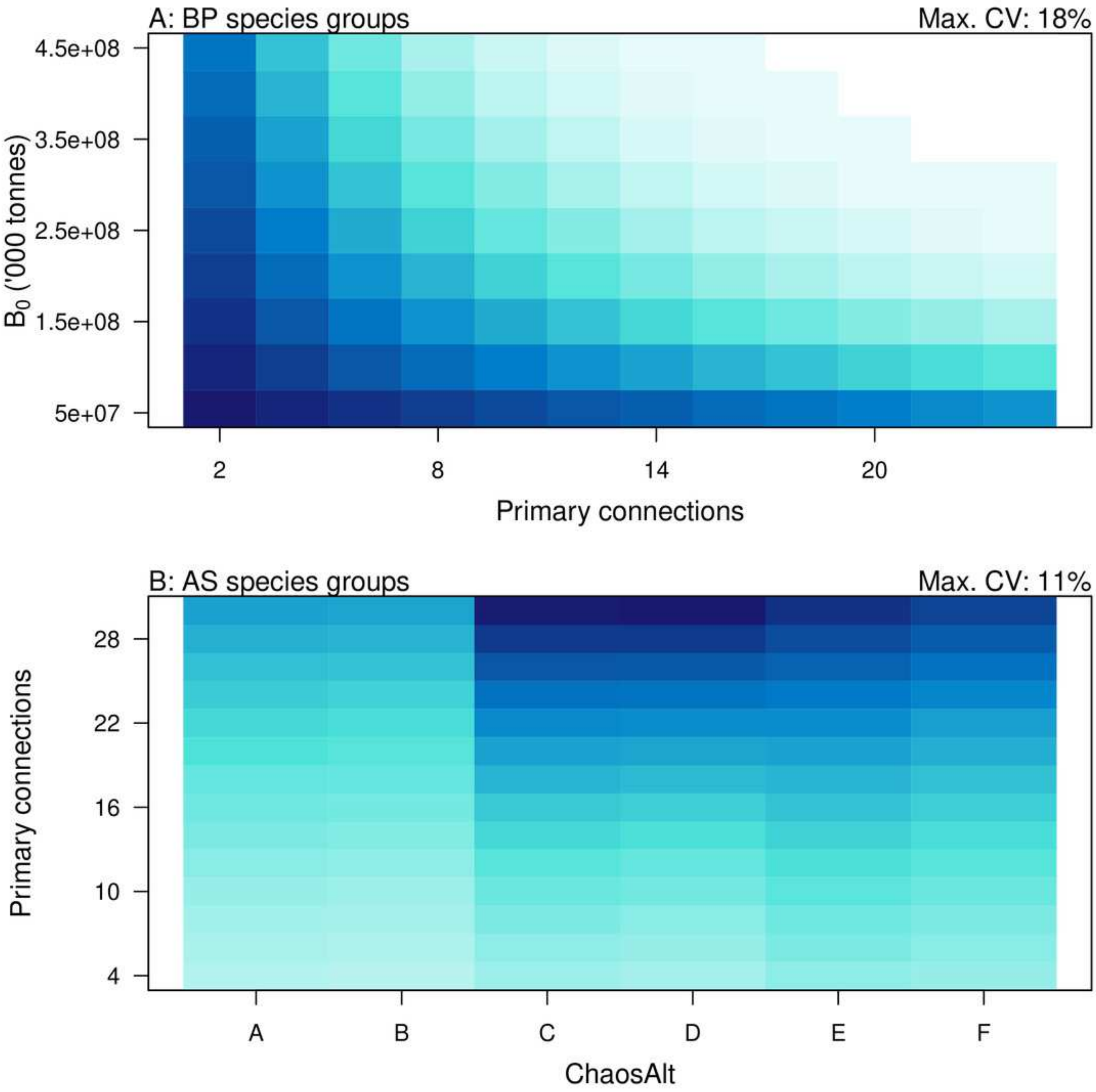
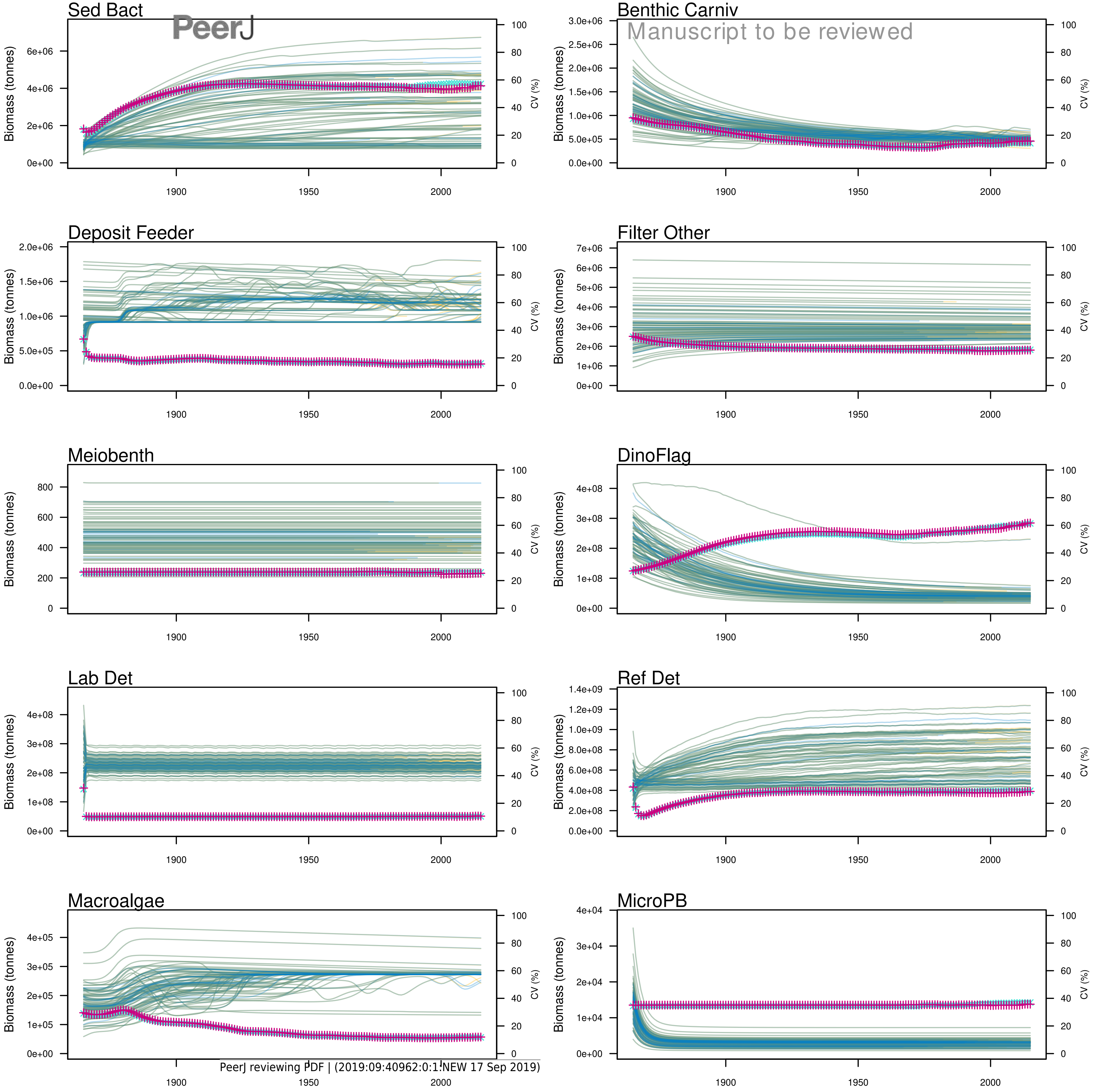


Figure 20(on next page)

Biomass trajectories from models with fishing included (blue lines) and no fishing (orange lines) for each species group, with CVs from across the model runs by time from fished models (aqua asterisks) and unfished models (cerise asterisks) overlaid and u


Sed Bact
Biomass (tonnes)
0e+00
2e+06
4e+06
6e+06
CV (%)
0
20
40
60
80
100
1900
1950
2000
Benthic Carniv
0.0e+00
5.0e+05
1.0e+06
1.5e+06
2.0e+06
2.5e+06
3.0e+06
Deposit Feeder
0.0e+00
5.0e+05
1.0e+06
1.5e+06
2.0e+06
Filter Other
0e+00
1e+06
2e+06
3e+06
4e+06
5e+06
6e+06
7e+06
Meiobenth
0
200
400
600
800
DinoFlag
0e+00
1e+08
2e+08
3e+08
4e+08
Lab Det
0e+00
1e+08
2e+08
3e+08
4e+08
Ref Det
0.0e+00
2.0e+08
4.0e+08
6.0e+08
8.0e+08
1.0e+09
1.2e+09
1.4e+09
Macroalgae
0e+00
1e+05
2e+05
3e+05
4e+05
MicroPB
0e+00
1e+04
2e+04
3e+04
4e+04

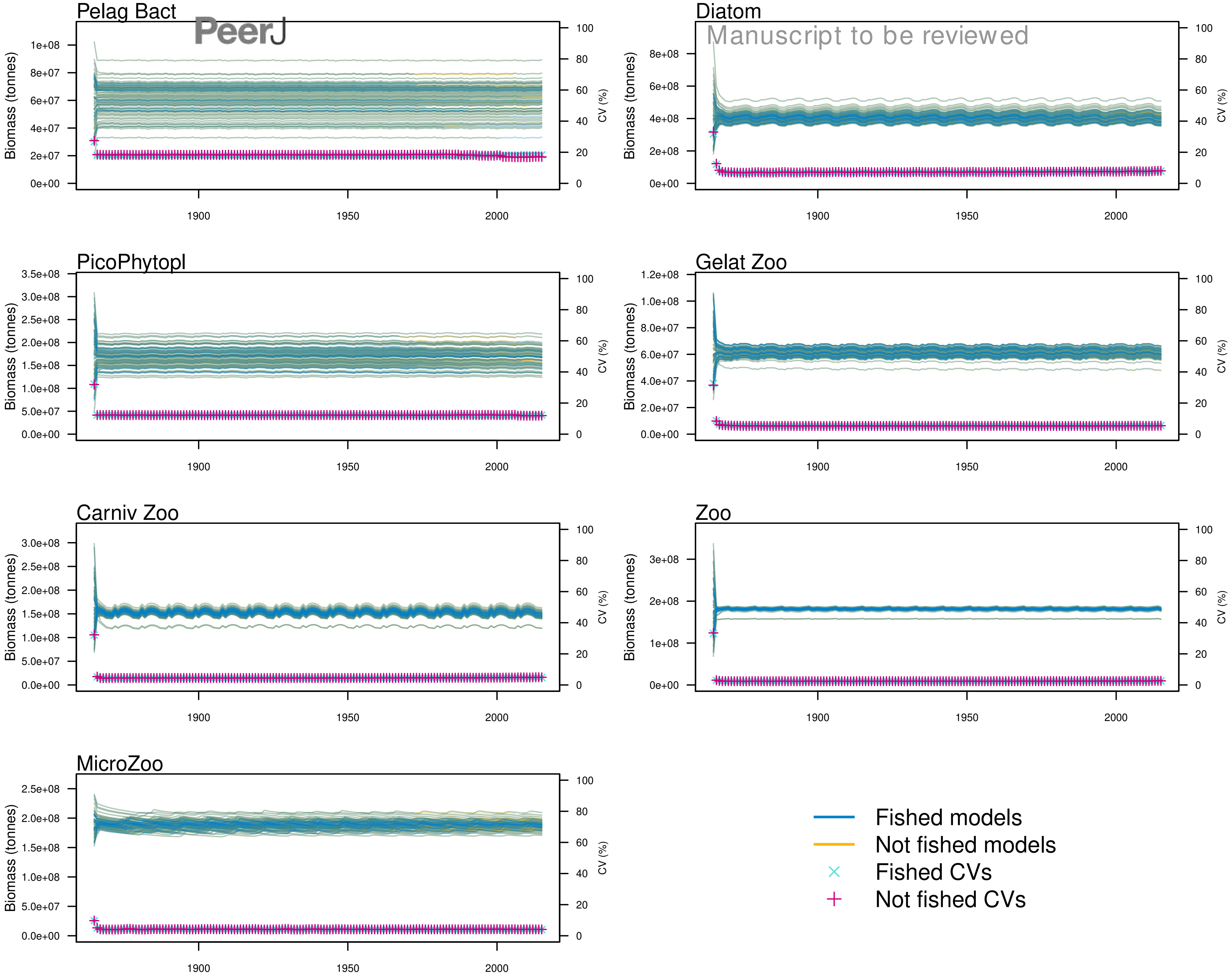
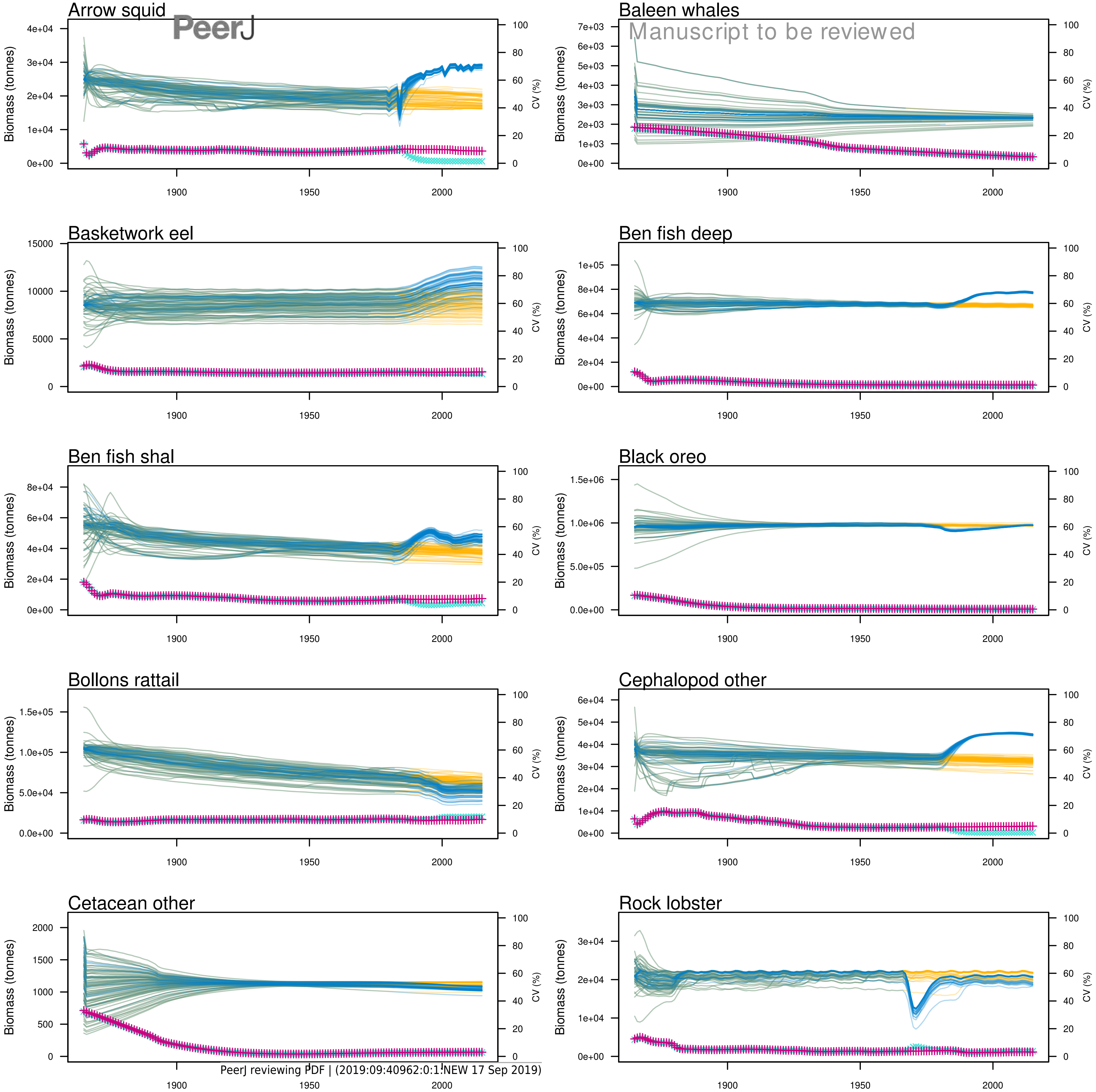
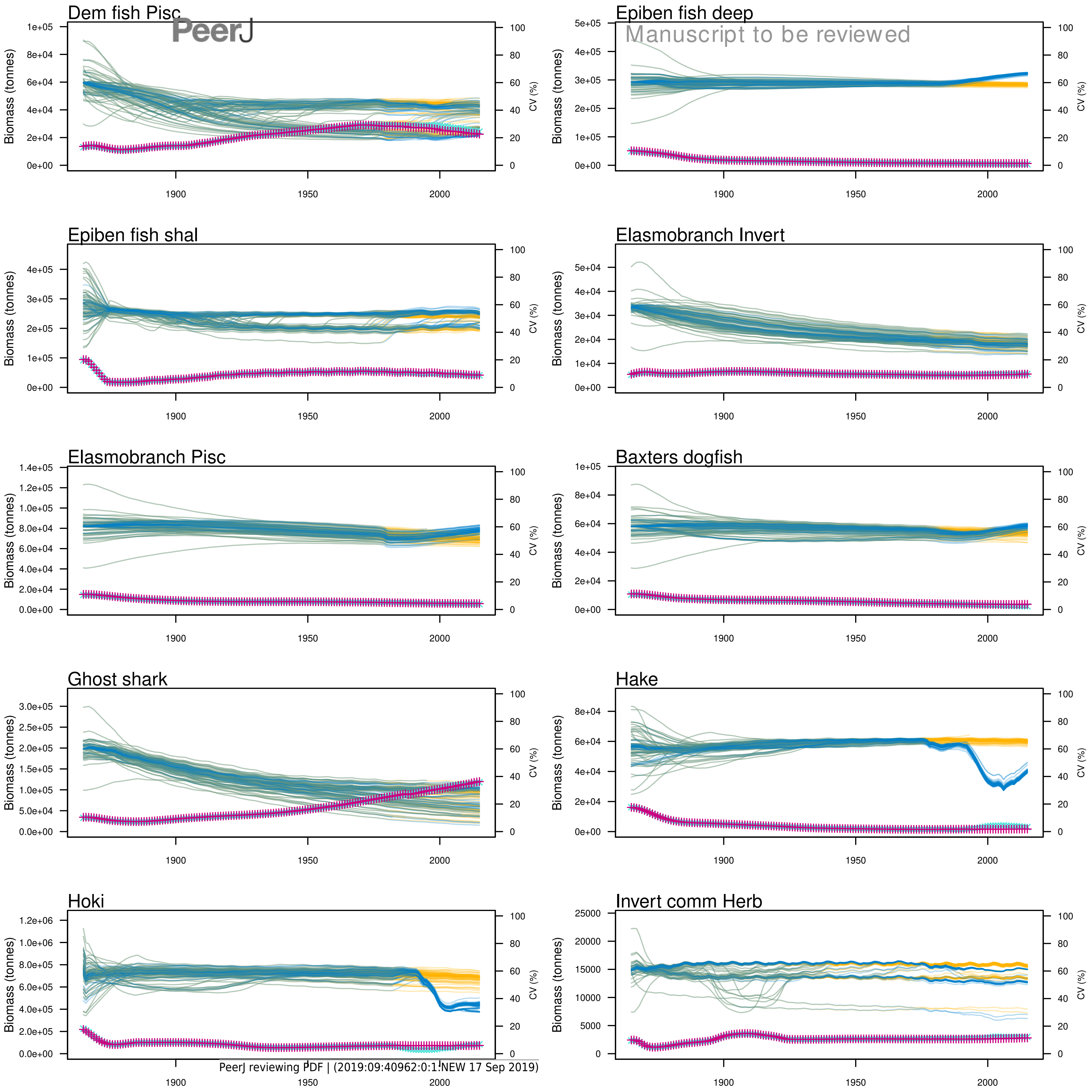
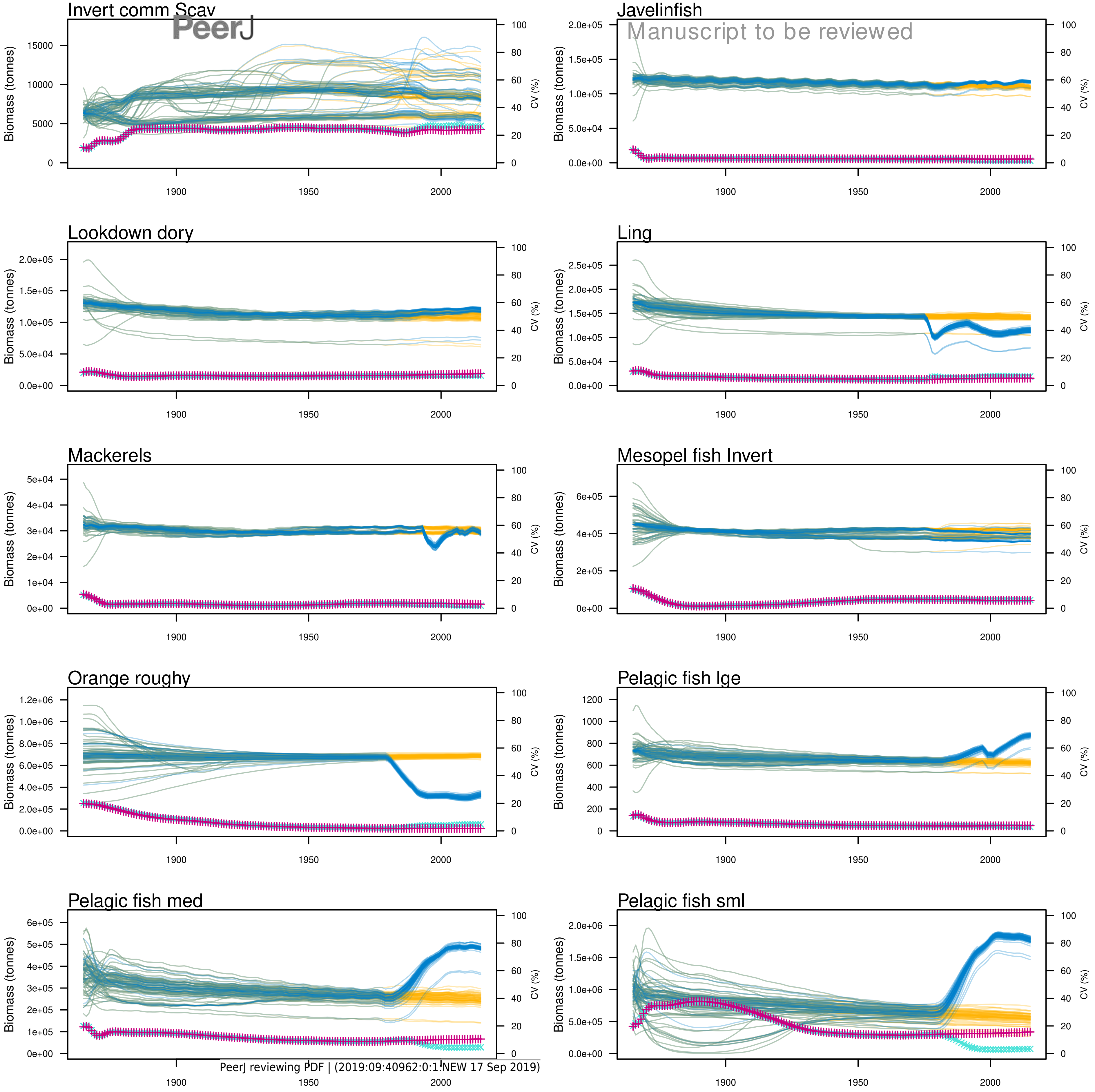

Pelag Bact
Diatom
PicoPhytopl
Gelat Zoo
Carniv Zoo
Zoo
MicroZoo
Biomass (tonnes)
CV (%)
0e+00
2e+07
4e+07
6e+07
8e+07
1e+08
2e+08
4e+08
6e+08
8e+08
0.0e+00
5.0e+07
1.0e+08
1.5e+08
2.0e+08
2.5e+08
3.0e+08
3.5e+08
2.0e+07
4.0e+07
6.0e+07
8.0e+07
1.0e+08
1.2e+08
1e+08
2e+08
3e+08
0
20
40
60
80
100
1900
1950
2000
Fished models
Not fished models
Fished CVs
Not fished CVs

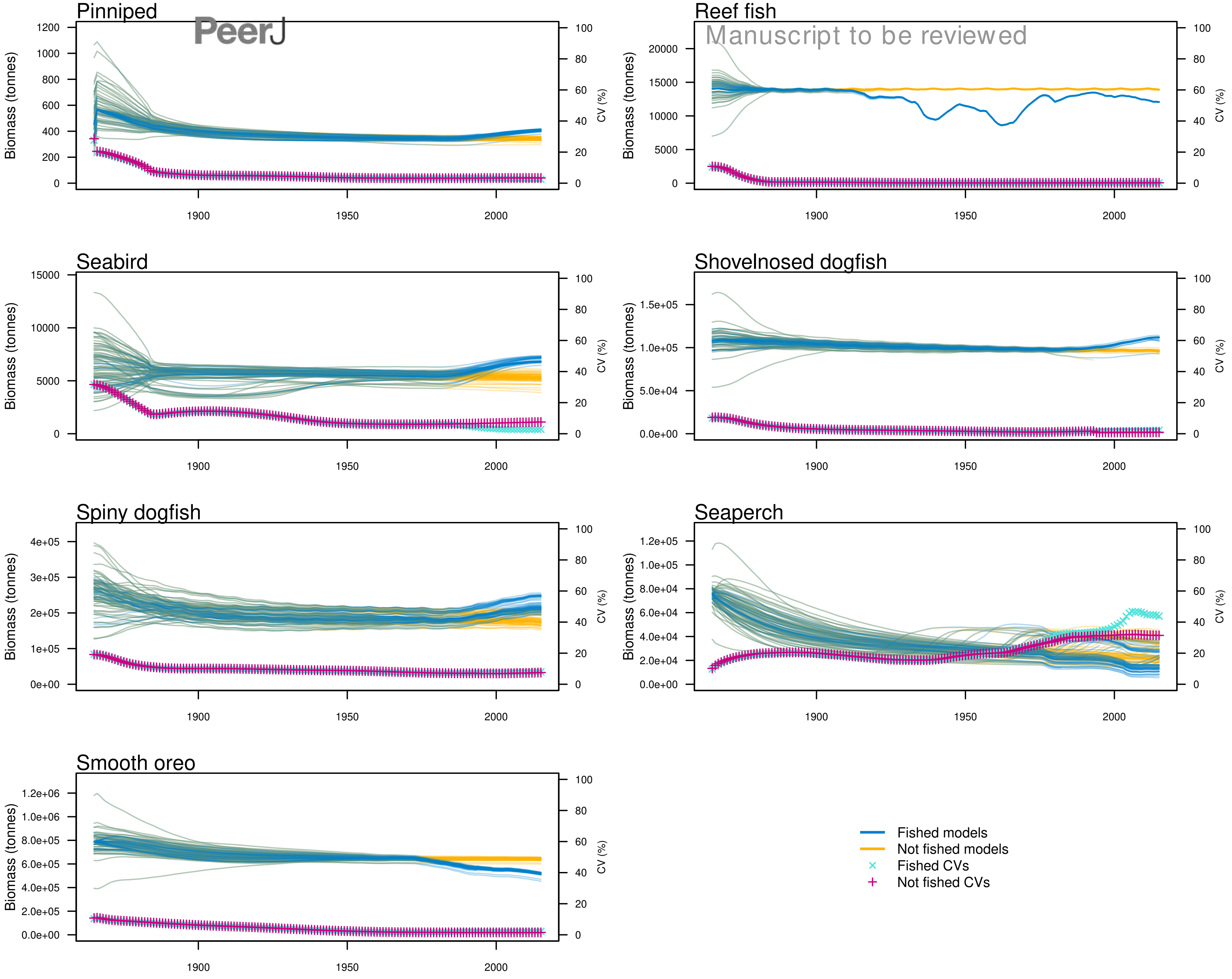
Figure 21(on next page)

Biomass trajectories from models with fishing included (blue lines) and no fishing (orange lines) for each species group, with CVs from across the model runs by time from fished models (aqua asterisks) and unfished models (cerise asterisks) overlaid and u


Arrow squid
Biomass (tonnes)
0e+00
1e+04
2e+04
3e+04
4e+04
CV (%)
0
20
40
60
80
100
1900
1950
2000
Baleen whales
Biomass (tonnes)
0e+00
1e+03
2e+03
3e+03
4e+03
5e+03
6e+03
7e+03
CV (%)
Basketwork eel
Biomass (tonnes)
0
5000
10000
15000
CV (%)
Ben fish deep
Biomass (tonnes)
0e+00
2e+04
4e+04
6e+04
8e+04
1e+05
CV (%)
Ben fish shal
Biomass (tonnes)
0e+00
2e+04
4e+04
6e+04
8e+04
CV (%)
Black oreo
Biomass (tonnes)
0.0e+00
5.0e+05
1.0e+06
1.5e+06
CV (%)
Bollons rattail
Biomass (tonnes)
0.0e+00
5.0e+04
1.0e+05
1.5e+05
CV (%)
Cephalopod other
Biomass (tonnes)
0e+00
1e+04
2e+04
3e+04
4e+04
5e+04
6e+04
CV (%)
Cetacean other
Biomass (tonnes)
0
500
1000
1500
2000
CV (%)
Rock lobster
Biomass (tonnes)
0e+00
1e+04
2e+04
3e+04
CV (%)


Dem fish Pisc
Epiben fish deep
Epiben fish shal
Elasmobranch Invert
Elasmobranch Pisc
Baxters dogfish
Ghost shark
Hake
Hoki
Invert comm Herb
Biomass (tonnes)
CV (%)
1900
1950
2000
0
20
40
60
80
100
0e+00
2e+04
4e+04
6e+04
8e+04
1e+05
1e+05
2e+05
3e+05
4e+05
5e+05
0.0e+00
2.0e+04
4.0e+04
6.0e+04
8.0e+04
1.0e+05
1.2e+05
1.4e+05
5.0e+04
1.5e+05
2.0e+05
2.5e+05
3.0e+05
2.0e+05
4.0e+05
6.0e+05
8.0e+05
1.0e+06
1.2e+06
5000
10000
15000
20000
25000


Invert comm Scav
Biomass (tonnes)
0
5000
10000
15000
CV (%)
0
20
40
60
80
100
1900
1950
2000
Javelinfish
0.0e+00
5.0e+04
1.0e+05
1.5e+05
2.0e+05
Lookdown dory
0.0e+00
5.0e+04
1.0e+05
1.5e+05
2.0e+05
Ling
0.0e+00
5.0e+04
1.0e+05
1.5e+05
2.0e+05
2.5e+05
Mackerels
0e+00
1e+04
2e+04
3e+04
4e+04
5e+04
Mesopel fish Invert
0e+00
2e+05
4e+05
6e+05
Orange roughy
0.0e+00
2.0e+05
4.0e+05
6.0e+05
8.0e+05
1.0e+06
1.2e+06
Pelagic fish lge
0
200
400
600
800
1000
1200
Pelagic fish med
0e+00
1e+05
2e+05
3e+05
4e+05
5e+05
6e+05
Pelagic fish sml
0.0e+00
5.0e+05
1.0e+06
1.5e+06
2.0e+06


Pinniped
Biomass (tonnes)
0
200
400
600
800
1000
1200
CV (%)
0
20
40
60
80
100
1900
1950
2000
Reef fish
Biomass (tonnes)
0
5000
10000
15000
20000
Seabird
Biomass (tonnes)
0
5000
10000
15000
Shovelnosed dogfish
0.0e+00
5.0e+04
1.0e+05
1.5e+05
Spiny dogfish
0e+00
1e+05
2e+05
3e+05
4e+05
Seaperch
0.0e+00
2.0e+04
4.0e+04
6.0e+04
8.0e+04
1.0e+05
1.2e+05
Smooth oreo
0.0e+00
2.0e+05
4.0e+05
6.0e+05
8.0e+05
1.0e+06
1.2e+06
Fished models
Not fished models
Fished CVs
Not fished CVs