Summing the parts: Improving population estimates using a state-space multispecies production model

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# Introduction

# Methods

## Model formulation

Trends in fish populations have frequently been described using state-space biomass dynamic models of the form

where is biomass at the start of year , is the catch through year , is production as a function of biomass, is an index of relative abundance in year from survey , is the time-invariant catchability coefficient for survey index , is process error, and is observation error. Statistical challenges aside, the most difficult aspect of this model to parameterize is the production function as it needs to capture changes caused by growth, recruitment, and natural mortality. Schaefer ([1](#ref-schaefer1954)) proposed a solution by applying the logistic equation to describe self-limiting growth,

where is the maximum per-capita rate of change and is the carrying capacity. That is, a populations’ intrinsic ability to grow () is limited by the size of the current population relative to the maximum biomass the system can support (). While this formulation offers an elegant description of single-species population dynamics, it assumes that density-dependent effects are solely caused by intraspecific competition and ignores the potential effects of other species inhabiting the same ecological area. We present an extension of equation (3) that attempts to account for intra and interspecific competition by assuming that density-dependent effects are incurred when the total biomass of multiple species, represented by , exceeds the capacity of the system,

While intrinsic rates of growth may vary across species, this formulation implies that the growth of all species is ultimately limited by the finite amount of energy in a region (i.e., as the population in the system increases towards , year-over-year growth of all species slows). Combining equations (1), (2), and (4), our model becomes

The inclusion of multiple species in the model permits the estimation of covariance. While covarying changes in observed populations may be described using observation errors, we assume that most covariance stems from population processes. We therefore assume that observation errors are independent and normal distribution such that , where the standard deviation parameter represents species and survey specific levels of observation error. A more flexible error structure is used to describe the process errors as ecological processes may contribute to species or temporal dependencies. Beyond the global limiting effect of , species interactions may elicit positive or negative population responses resulting from direct or indirect associations. We therefore apply the multivariate normal distribution to account for the possibility that process errors are not independent across species. Deviations from expected production may also display temporal dependence if the factors contributing to the process errors change slowly through time. Such inertia may cause positive or negative process errors to persist across several years. A first-order autoregressive (AR1) process was therefore applied to account for temporal dependence. Both sources of dependence are modeled using a multivariate AR1 process where

and

The degree of temporal correlation is controlled by , where values between 0 to 1 represent low to high correlation, and species-to-species correlations are described by , where values between -1 to 1 represent negative to positive correlation. This is a flexible structure that allows for the testing of alternate hypotheses that process errors are independent through time or across species (i.e, or ). The possibility that process errors are similarly correlated across all species may also be tested by estimating only one parameter. Finally, the magnitude of the process error deviations are controlled by the species-specific standard deviation parameters, .

Finally, the formulation allows the fitting of covariates that may describe an underlying linear effect. Two options were implemented, one that affects the process errors by substituting in equation (5) with , and another that affects the carrying capacity by substituting in equation (5) with . The idea is that some factors may affect positive or negative changes in the populations while others may affect change in the total carrying capacity of the system. A covariate option for intrinsic rates of increase was not implemented as one goal of this model is to obtain estimates of this vital rate, which is not expected to change rapidly as it is shaped by natural selection ([2](#ref-hutchings2021)).

## Statistical framework

This model was implemented using template model builder (TMB; [3](#ref-kristensen2015)), which is package for R ([4](#ref-R)) that enables the fitting of complex nonlinear random effects such as the latent variable in state-space biomass dynamic models (equation (1)). Such variables are not directly measured but are inferred indirectly via observed values. Data fitting is accomplished using a combination of Laplace approximation and automatic differentiation to evaluate the joint likelihood ([3](#ref-kristensen2015)). Like the production model descried by Pedersen et al. ([5](#ref-pedersen2017)), both frequentist and Bayesian inference of model parameters are possible. In development, we found that estimation was generally more successful when vaguely informative priors are specified as parameters were, in some cases, not identifiable when unconstrained.

## Case study

### Data

### Priors

# Results

# Discussion

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# Figures