What do Bayesian state-space models tell us about fish stock structure?: multiple species, multiple years of data, and multiple survey types may not mean multiple stocks.

Kelli F. Johnson, Kerim A. Aydin, and André E. Punt

Todo: The abstract will go here.

##### keywords

Alaska, Atka mackerel, Pacific cod, walleye pollock

# Introduction

The first step in the management of natural resources is to determine the management unit, which will depend on the management objectives. Thus, management units should evolve in concert with changing management objectives (Begg and Waldman, 1999). Historically, management units for exploited marine fishes (i.e. stocks) lacked biological foundations and instead were politically based. Currently, stock boundaries for many fish stocks remain unchanged despite the plea for better aligning the spatial scale of management with the natural scale of targeted populations in the 10 commandments for ecosystem-based fisheries scientists (Francis *et al*., 2007). The predominance of political boundaries is reflected in the recent defintion of the management unit by the International Council for the Exploration of the Sea: “a geographically delinated fishery resource that is based on practical or jurisdictional boundaries for operational stock assessment and fishery management, which may or may not reflect biological population structure” (ICES, 2013). Research and application of methods that define stock boundaries based on biology are becoming increasingly needed as managers shift from the World War II era focus on single species maximum sustainble yield to maximum optimal yield, which can incorporate biological, economic, and social objectives (Rothschild, 1973; Sissenwine, 1978).

Few marine fish species lack evidence of complex spatial structure (Conover *et al*., 2006; Cope and Punt, 2009). Stephenson (1999) even goes so far to claim that all distinct spawning groups should be considered stocks until proven otherwise. Furthermore, stock structures should not be seen as static; species ranges are predicted to shift with respect to depth and latitude as oceans warm in response to climate change (Perry *et al*., 2005; Dulvy *et al*., 2008; Nye *et al*., 2009), potentially increasing the mismatch between political and biological stock boundaries. Thus, accounting for spatial structure by properly identifying stock boundaries is necessary for several reasons, including but not limited to the i) fair allocation of catch among competing fisheries and/or nations (Kutkuhn, 1981; todo: citation), ii) protection of nursing and spawning areas (Smith *et al*., 1990; Stephenson, 1999), iii) development of optimal harvest and monitoring strategies (Begg *et al*., 1999a; Frank and Brickman, 2000), iv) reduction of localized depletion (todo: citation), v) proper identification of choke species (todo: citation, todo: ANDRÉ is this a duplication of localized depletion), and vi) sustainability of prey resources (Bertrand *et al*., 2012).

Spatial structures used to delineate management boundaries of terrestrial organisms typically coincide with abrupt changes in topography or visible barriers to migration. In contrast, marine environments often lack clear physical boundaries and areas of abrupt physical changes (e.g. canyons and seamounts) or changing hydrography (e.g. fronts) are characterized by high productivity limiting their ability to define boundaries in the traditional style (Olson *et al*., 1994; Allen *et al*., 2001; Ciannelli *et al*., 2004). To further complicate things, areas of high productivity will only be beneficial to those organisms that can use it to enhance their growth, while those that are not equipped will find it as a barrier (Olson *et al*., 1994). Thus marine barriers may be specific to life-history stage and vary in space and time (todo: citation). For example, three extreme currents (i.e. Alaska Coastal Current, Alaskan Stream, and Aleutian North Slope Current) work together with bathymetric features, namely Aleutian Islands (AI) passes, in the north east Pacific Ocean to define the major physical attributes of the hydrography. East of Samalga Pass, the Alaska Coastal Current transports warm fresh water from the Gulf of Alaska (GOA) to the Bering Sea (BS), while west of the pass, colder more oceanic water is transported east by the Alaskan Stream (Hunt and Stabeno, 2005). Passes to the west of Samalga Pass become wider and deeper along the narrow continental shelf until Amchitka Pass. Here, the Alaskan Stream, the mains source of inflow to the Bering Sea, turns northwestward. Westward of Amchitka Pass, the islands are small but seperated by deep canyons, followed by a broad shallow shelf flanked by Kamchatka Strait, the deepest of the straits and the main source of Bering Sea outflow (Stabeno and Reed 1994).

todo: needs a transition and some relevance to stock structure (Loggerwell *et al*., 2005).

Currently, no one method properly identifies all stocks. Thus, integrating the results from a suite of techniques to address multiple aspects of the biology and life-history characteristics of marine fishes increases the likelihood of detecting relevant variation between stocks (Hohn, 1997; Waldman *et al*., 1997; Coyle, 1998; Begg *et al*., 1999b; Abaunza *et al*., 2004; Hatfield *et al*., 2005) (todo: trim down the number of references). Several available techniques require a substantive amount of costly data, necessitating a balance between accuracy and efficiency (Hilborn and Walters, 1992). Thus, techniques that use data routinely collected for assessment and management purposes (i.e. life-history parameters) are advantageous. As a bare minimum, catch data and distribution data from fishery-independent surveys, if available, can provide baseic information on the areas used by a stock. Nevertheless, with the development of fisheries science and as fisheries increase in value, increasing amounts of data are typically collected for each life-history stage providing further information on stock characteristics such as growth, survival, age-at-maturation, and fecundity (Ihssen *et al*., 1981; Pawson and Jennings, 1996; Maunder and Punt, 2013). Life-history data can provide inferences about genotypic variation resulting from environmental and anthropocentric influences by categorizing phenotypic expressions. In short, using life-history data to deliniate stock can provide a good starting point for more advanced stock identification techniques (e.g. biochemical, immunological, serological, behavioural, morphometric, meristic, mark-recapture, etc.), while being cost effective and efficient (Begg et al, 1999b).

Unfortunately, fisheries data are subject to both observation and process error, which can lead to complicated analyses. Observation error can originate from many sources, including: i) imperfect detection, ii) environmental conditions hindering the logistics and replicability of the study, iii) human error, iv) discarding, v) small sample sizes, and vi) non-independent sampling (Doubleday and Rivard, 1983; Alverson *et al*., 1994). Whereas, process error is the variation in true population size due to stochastic environmental conditions. Biologists are often primarily interested in quantifying process error, as opposed to observation error, which is often seen as a nuisance. Approaches to accommodate both process and observation error in a single framework are limited and few methods fully account for the probability structure created by their joint presence. Typically, one or the other is ignored, assuming either that the observations are perfectly observed or the process is purely deterministic. Ignoring one or the other can lead to biased parameter estimation (todo: citation), invalid hypothesis testing (todo: citation), and biased predictions (todo: citation).

State-space models can simultaneously estimate process and observation error making them ideal for ecological data. Their use in ecology began with time-series data for single populations (Staples, Taper, and Dennis, 2004; Dennis *et al*., 2006) and later extended into two-dimensional space for movement data (Jonsen, Myers, and Flemming, 2003) and multiple subpopulations (Ward *et al*., 2009) and species (Mattsson *et al*., 2013). Multivariate time-series analysis is one way to detect spatial patterns of correlation and synchrony across multiple locations (todo: citation) and can provide inferences on stock structure based on ecological differences. More specifically, Bayesian multivariate state-space models provide posterior probabilities of growth rates, density dependence, process variability, and observation variability using time-series data from multiple sites (Hinrichsen and HoMEs, 2009; Ward *et al*., 2010) (todo: these references are not Bayesian). The method is extremely flexible and can accommodate several population growth models, unequal sampling effort, missing data, multiple stock structures, density dependence, and data from multiple species. Here we present an ecological assessment of stock structures for three species, walleye pollock (*Theragra chalcogramma*; hereafter referred to as pollock), Pacific cod (*Gadus macrocephalus*; hereafter referred to as cod), and Atka mackerel (*Pleurogrammus monopterygius*; hereafter referred to as mackerel) in the north east Pacific Ocean using Bayesian multivariate autoregressive state-space models.

Pollock, cod, and mackerel are important both ecologically and commercially in the BSAI and GOA LMEs. Pollock and cod represent the two largest fisheries by weight in all of Alaska (1,310,330 and 329,040 (t), respectively; st.nmfs.noaa.gov). Furthmore, pollock and mackerel are the main prey for cod, comprising approximately 19% and 27% of total cod stomach contents, respectively (Ortiz, 2007). As well, pollock and mackerel are the two most common prey species (frequency of occurrence (FO) 46.4% and 39.6%, respectively) of the federally endangered Steller sea lion (Eumetopias jubatus; SSL), with cod being the fourth most common (FO = 16.1%) (Sinclair and Zeppelin, 2002). Currently, pollock are managed as four stocks (BS, AI, GOA, and Bogoslof), cod is managed as three stocks (BS, AI, and GOA), and mackerel is managed as two stocks (BSAI and GOA), although there is no stock assessment for mackerel in the GOA region because there is no targeted fishery. Nevertheless, evidence for stock structures is cited as being equivocal and stock assessment documents suggest further research and analysis regarding stock structure as a research priorities (todo: citation BS pollock assessment; BS p cod assessment; BSAI mackerel assessment).

The AIs are complex and the least predictable of the three management areas. Thus, it may be most appropriate to delineate stocks based on current patterns, such as Samalga Pass () rather than politically established management boundaries (i.e. ; Pacific Fisheries Management Council, ?? todo: update this citation). Furthermore, declines in pinnipeds and marine bird populations are often linked to decreases in prey availability, resulting from commercial exploitation or climate change (NRC, 1996; Loughlin and York, 2000; NRC, 2003; DeMaster *et al*., 2006; Hennen, 2006). Reductions in prey abundance and quality is one of the more supported hypotheses for the decline in SSL abundance in western and central Alaska since the 1960’s (todo: citation). Studies revealed that diets were more similar between island rookeries in close proximity to one another (Sinclair and Zeppelin, 2002). Thus, decreasing the risk of localized prey extinction may be important for SSL recovery and understanding the stock structure of these three fish species is an important task, not to mention a federally mandated one according to the Endangered Species Act and the Sustainable Fisheries Act.

Bayesian state-space models were used here to determine localized growth rates and process variability for three species (pollock, cod, and mackerel) in the BS, AIs, and GOA regions, while testing various hypotheses regarding localized stock structure. The hypotheses are based on known current patterns. The best model was chosen using model-selection criteria. The method should be useful to researchers looking to esablish stock structures that will lead to robust ecosystem based fisheries management and minimize the chances of localized depletion for multiple species in a single analysis.

## Data

todo: Briefly describe the ecosystems being modeled, but don’t make it too long

Survey data were collected by the Alaska Fisheries Science Center of the National Marine Fisheries Service from 1982 to 2012 during the annual eastern BS shelf bottom trawl survey and the triennial GOA and AI bottom trawl surveys. Data serves to provide estimates of biomass, abundance, and population structure of groundfish and crab to the the North Pacific Management Council.

The BS surveys covered depths up to 200 *m* from the Alaskan Peninsula north to (N) (Bakkala, 1993). The AI surveys covered depths up to 500 *m* along the north side of the AIs from Unimak Pass (W) westward to Samalga Pass (W) and on both sides of the AIs from Samalga Pass to Stalemate Bank (E) (Harrison, 1993). The GOA survey covered depths up to 1000 *m* from Samalga Pass to Dixon Entrance () (Britt and Martin, 2001). Surveys in the AIs were conducted in 1983, 1986, 1991, 1994, 1997, 2000, 2002, 2004, 2006, 2010, and 2012. Surveys in the GOA were conducted in 1984, 1987, 2990, 1993, 1996, 1999, 2001, 2003, 2005, 2007, 2009, and 2011.

All surveys employed a stratified random sampling design, with intensified sampling near the Pribilof Islands and St. Matthew Island. Tows of 30 min (estimated on bottom duration) at speeds of 5.6 were conducted at each sampled station. Todo: add more survey information here, particularly the difference in trawl gear with a reference.

For each tow, species composition of the catch was determined and catch per unit effort (*CPUE*) was calculated as the weight of the catch (*kg*) divided by the area swept (*ha*) for a given trawl. A value of 0.001 was added to all station *x* year combinations for each species where the abundance of the desired species was zero, if the station had at least one positive abundance during the study. Station *x* species combinations were removed from the analysis if they failed to generate a positive CPUE over the course of the study.

## Bayesian multivariate autoregressive state-space model

Multivariate autoregressive state-spaces models were used to model each hypothesized stock structure and estimate their respective population parameters. Models were discrete, stochastic, and lacked any age structure. Growth rates were modeled using an exponential function described by   
 where ; is the population abundance at time *t*; and is the deterministic per-unit-abundance growth rate in population density (Dennis et al., 1991). Exponential growth can be a valid assumption for depleted populations far from carrying capacity. Pollock and cod are heavily fished species, therefore the biases associated with the assumption of exponential growth are assumed to be minimal in this specific application. Todo: provide a rational for mackerel. Here, process error () represents stochastic deviations from the long-term trend due to environmental effects. Process error was assumed to be normally distributed with mean of zero and a constant variance. After defining as the growth process for a single subpopulation, the growth process can be expressed as   
 which represents a discrete-time random walk with drift. The model becomes multivariate by extending the equation to model *m* unknown subpopulation *x* species combinations with potentially correlated process error. Observations are distinct for each subpopulations *x* species combination, but process error can be correlated between species. Using capital letters for vectors and bold letters for matrices, the equation becomes   
 where is an x 1 vector of stochastic growth rates and is an x 1 vector of serially uncorrelated process error with a mean of zero and x covariance matrix, **.**

The observed values of *logCPUE*, , are related to the true log abundances, , through   
 where is a vector of length , representing the mean bias between sites, is an x matrix of 0s and 1s, translating the subpopulations at time into observations at time ; and is a vector of serially uncorrelated observation errors with a mean of zero and x covariance matrix . Observation error can include several types of error: sampling error, measurement error, location error, or biases in availability. If ignored, measurement error can create bias in results, but it does not contribute to error in the predictions of future abundances only observations of those abundances.

## Candidate models

Hypothesized stock structures were determined a priori based on the life history of the included species and the hydrography of the area. The following hypotheses were based on delinating areas between AI passes and GOA fronts and grouping them into various configurations (Figure 1).

**Management** (*m* = 3 *x* 3): sites were grouped according to current management boundaries for the BS, AI, and GOA.

**Independent** (*m* = 7 *x* 3): each of the seven areas represents its own subpopulation.

Within the above hypotheses, we tested three levels of process variance complexity ((i) equal process variance, (ii) unequal and uncorrelated process variance, and (iii) unequal and correlated process variance) and two levels of observation variance complexity ((i) equal and (ii) unequal and uncorrelated). We did not test for unequal and correlated observation variance because observations were collected independently at each site without repetition. Furthermore, we tested for correlations between species with respect to process error variance and equality with respect to observation error variance.

## Priors

The priors for observation and process error variance were specified as an inverse gamma distributions. The distribution is a two-parameter (i.e. shape and scale) family distribution located on the positive real number line. The shape and scale parameters for the priors were informed by analyzing sampling variation for all stations within the North Pacific Fishery Management Council that had multiple tows in a given year.

Given that measurements were not available for each subpopulation, only observations of those subpopulations, the initial simulated logCPUE values () were drawn from a random normal distribution with a mean of zero and a standard deviation of 0.01. Priors for elements of the vector were also drawn from a random normal distribution with a mean of one.

Priors were the same for all models except when was unequal and correlated. When the process variances were correlated we used the Wishart distribution. The Wishart distribution is guaranteed to produce positive definite draws, provided that , where the smaller is, the more the variability (Kollo and Ruul, 2003). The Wishart was parameterized with an for all models. Under the assumption that the priors for each parameter are independent, given that a Wishart distribution is used when variances are correlated, the priors were constructed individually and the joint prior is the product of the priors for each parameter:   
 where is the prior for parameter (; where is the number of parameters in model ) in the vector .

## Estimation

The probability that a given hypothesis is true () is conditioned on the data, (), and is given by   
 where is the prior probability density for the hypothesis and is the likelihood function for the data evaluated at . Given the problem at hand, the likelihood function was evaluated as:   
 also known as the normal density function.

It can be extremely difficult if not impossible to obtain an analytical solution of the density function, thus numerical procedures are often necessary. To overcome this limitation most analyses use either Markov Chain methods (Gibbs sampler or Markov Chain Monte Carlo) or importance sampling. We used Markov Chain Monte Carlo (MCMC) to obtain posterior distributions of the parameters of interest. The Gibbs sampling program was implemented in R using Just Another Gibbs Sampler (JAGS), a program that steps through the unkown parameters one at a time conditional on the current values of all the other parameters and then samples a random value from the poster distribution.

## Model fitting

All models were fit with three chains with each chain having a final sample size of ? iterations. Convergence of the algorithms was checked using trace plots of the parameters, plots showing correlations between parameters, and Gweke statistics for convergence (CITATION).

## Model selection

Deviance Information Criteria (DIC) was used to determine the best model of the hypothesized models. Deviance information criterion (DIC) is useful in Bayesian model selection when the posterior distribution is approximately multivariate normal and results were obtained using MCMC sampling. The formula is as shown,   
 where smaller values indicate a better fit of the model to the data.