

Using multivariate autoregressive state-space models to inform Pacific cod *Gadus macrocephalus* stock structure in the Aleutian Islands, Alaska

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Abstract

A major assumption of management recommendations and one that is rarely valid is that populations are discrete homogeneous units. Furthermore, population units are rarely defined on a scale that is of relevance to managers. Here we use a newly developed statistical technique to assess the synchrony of stock population dynamics for four hypothesized stock structures of Pacific cod *Gadus macrocephalus* in the Aleutian Islands, Alaska. Using data already collected for fisheries managers, we used a multivariate state-space framework to model unknown states where the states are subject to process error and the data is subject to observation error. Akaike's Information Criterion was used to provide inference on the stock structure best supported by the data. Pacific cod in the Bering Sea and Aleutian Islands is currently managed as a single stock despite evidence for genetic differentiation. We based our hypothesized stock structures on supposed drivers for this genetic variation between Pacific cod in the Aleutian Islands and the Southern Bering Sea. Model selection results strongly support a stock structure with at least two distinct stocks, one east of Samalga Pass and one west of the pass. Weaker support also exists for an additional stock west of Adak Strait, creating three distinct stocks: (1) west of Adak Strait, (2) central Aleutians between Adak Strait and Samalga Pass and (3) west of Samalga Pass.

Introduction

Fish species rarely move freely throughout their biological ranges. Rather, species form discrete populations, or stocks, which exhibit varying degrees of isolation from each other in space, time or both. Several factors (e.g., demographic and life history variability, habitat patchiness, environmental change, genetic structuring and adaptability) may lead to species heterogeneity, or more specifically, unique stock level population dynamics (?). The majority of management recommendations are based on the assumption that populations are discrete homogeneous units. Therefore, knowing the stock structure of a species and how growth and mortality differ between stocks is integral to effective harvest and conservation management (???).

Many diverse techniques exist to infer stock structures in marine fishes. The shared goal of all techniques is to identify semi-discrete groups of fish with some definable attributes of interest to managers. How stocks are defined and the technique(s) used to identify them ultimately depends on the management question of concern and the spatial and temporal scales at which it applies. No one technique possesses the ability to discriminate between all fish stocks. Most techniques attempt to characterize genetic and/or phenotypic variation. Genetic variation is useful in measuring evolutionary differences between stocks (?) and phenotypic variation is useful for measuring differences in stocks due to short-term environmental effects (?). To maximize the likelihood of correctly defining and identifying stock structure Begg and Waldman ? suggest using multiple techniques.

Pacific cod *Gadus macrocephalus* are a transoceanic demersal fish ranging in the eastern North Pacific from California to the Bering Sea and in the western North Pacific from the Okhotsk Sea to the Yellow Sea (?). Historically, the species has supported both large- and small-scale commercial fisheries throughout its range. In 2010 global marine capture fisheries for Pacific cod represented the 28th largest fishery by weight in the world with 63% of catches coming United States (US) fisheries (www.fao.org), of which 78% were caught in the Eastern Bering Sea (EBS) and Aleutian Islands (AI). In addition to supporting a major commercial fishery, Pacific cod is ecologically important in the EBS and AIs as a predator of pollock,

shrimp and snow crab (?) and as prey for fish, sea birds and marine mammals (??). Specifically, Pacific cod is one of the four most important prey items for the federally endangered Steller sea lion *Eumetopias jubatus* (?).

In the Bering Sea Aleutian Island (BSAI) management unit, Pacific cod are managed as a single stock, and have been since the introduction of the Magnuson-Stevens Fishery Conservation and Management Act in 1977. Historically justification for managing the fishery as a single stock came from tagging studies documenting migration between the AIs and the EBS (?) and a lack of genetic differentiation between the two regions (?). Thanks to advances in genetic techniques and increased sample sizes, differentiation between the two areas is now well documented (????). Furthermore, recent analyses detected genetic differences within the EBS and the AIs (?). Despite evidence for complex stock structures, management efforts by the North Pacific Fishery Management Council (NPFMC) to sustainably manage the BSAI Pacific cod fishery and to conserve the BSAI community structure currently disregard the potential for heterogeneous Pacific cod population dynamics.

Here we present an ecological assessment of stock structures in AI Pacific cod from multivariate autoregressive state-space models. Multivariate time-series analysis is one way to detect spatial patterns of correlation and synchrony across different sites (?) and provide inferences regarding stock structure based on ecological differentiation. Inferences can be made regarding which sites share population dynamics, act independently of each other or are independent but correlated. Multivariate time-series analysis is a hopeful method for providing information on stock structure because it draws inferences from data already collected for fisheries management and can test hypotheses about stock configuration and biological parameters while including both process and observation error (?). Hypothesized stock boundaries tested in this analysis are based on documented genetic variation and the proposed drivers for that variation.

Methods

Data collection

The Aleutian Islands are an extensive archipelago comprised of 14 large and hundreds of small volcanic islands. The archipelago extends approximately 1,200 mi (1,900 km) westward from the Alaska Peninsula along a relatively narrow continental shelf separating the Bering Sea and the Pacific Ocean. It is the world's only longitudinally orientated high-latitude island archipelago. Strong currents flow northward through numerous deep passes resulting in mixing of deeper and surface waters and affecting salt, nutrient and plankton concentrations. Vertical mixing can vary on small spatial and temporal time-scales leading to complex patterns of prey concentrations for seabirds and other predators. The narrow shelf results in close proximity of onshore, near-shore and offshore systems leading to distinctly different ecosystem biology than the EBS and the Gulf of Alaska (GOA).

Bottom trawl surveys of groundfish resources have been conducted in the AI since 1980. United States-Japan cooperative surveys were conducted during the summers of 1980, 1983 and 1986 and US surveys conducted by the National Marine Fisheries Service (NMFS) were conducted in the same areas in 1991, 1994, 1997, 2000, 2002, 2004, 2006, 2010 and 2012. The most recent survey in 2012 constitutes the 12th year of the full time-series. The survey area extends along the north side of the Aleutian Islands from Akutan Pass (165° W) to Stalemate Bank (170° E), west of Attu Island and along the south side of the archipelago from the Islands of the Four Mountains (170° W) to Stalemate Bank. Surveys include waters ranging from near-shore to 500 (m) deep.

The AI survey area (64,415 km²) includes four of the NPFMC statistical areas: the Southern Bering Sea (SBS) district of the Bering Sea Subarea (518) and the Eastern, Central and Western Districts of the Aleutian Subarea (541, 542, 543, respectively) (Figure 1). The four areas are further divided into 45 area-depth sampling strata.

The survey design is a stratified random sampling scheme consisting of 450 stations with approximately 15 minute tows (estimated on-bottom duration) at speeds of $5.6 \text{ km} \cdot \text{h}^{-1}$ at each station. The AFSC bottom trawl uses a Poly Nor'Eastern high-opening bottom trawl made of 12.7 cm stretched mesh polyethylene netting, with a 24.2 m roller gear footrope in turn made with 36 cm rubber bobbins separated by 10 cm rubber disks (?). Catches of fish and invertebrates were sorted to species or to species aggregate, weighted and enumerated according to standard AFSC/Resource Assessment and Conservation Engineering (RACE) Division protocols (?).

Yearly survey results were provided as mean species weight per unit effort (CPUE), for each strata ($\text{kg} \cdot \text{ha}^{-1}$) (Figure 2). For each species, CPUE was calculated by dividing catch weight (kg) by the area swept in that trawl (ha). Mean CPUE for each strata was calculated as the mean of individual tow CPUEs (including zeros) within the stratum. For all analyses in this study data (mean CPUE) was log transformed to stabilize the variance. Because some strata contained tows with zero biomass a value of one was added to the data to facilitate log transformation (?). Zeros were not ignored because they were believed to represent true values where Pacific cod were not caught in successful tows.

Multivariate autoregressive state-space model

We used the multivariate state-space (MARSS) framework to model hypothesized stock structures, while simultaneously estimating process and observation error (??). Broadly, process error accounts for misspecification in the population dynamics model. Here, process error appears in the growth rate term and attempts to correct for the inability of the model to account for temporal variability in growth rate due to environmental stochasticity. Because the model is written as a function of log mean CPUE, process error is a multiplicative process. Observation error accounts for our inability to sample strata with absolute precision. Observation error can be attributed to several sources (e.g., inaccurate measurements and sampling only a portion of the population) but sources are confounded and cannot be estimated independently. However, state-space models can separate process and observation error making them ideal for empirically collected ecological data.

The MARSS model consists of two equations, one for the population process (Equation 1) and one for the observation process (Equation 2). We use n to represent the number of survey strata and m to represent the number of unknown stocks. For the process model, X_t is a vector of length m representing the true logarithmic stock size in year t ; B is an $m \times m$ matrix specifying density dependence within and between stocks; U is an m -element vector of stock growth rates; and w_t is a vector of length m representing the process errors in year t . We assumed no density dependence in our models and specified the diagonal of the B matrix to 1 and the off-diagonals to 0. Pacific cod is a heavily fished species, assumed to be far from carrying capacity (?). Estimates of B and u are often confounded and by specifying one or the other we avoided major convergence issues. Process errors are assumed to be serially uncorrelated in time and multivariate normal with mean zero and covariance defined by the $m \times m$ Q matrix. For the observation model, Y_t is a n -element vector containing observations of log mean CPUE at each site for each year t ; Z is an $n \times m$ matrix of 0s and 1s, translating the observations in year t to stock size in year t ; A is an n -element vector representing biases between strata; and v_t is a vector of length n representing the observation error in year t . Observation errors are also assumed to be serially uncorrelated in time and multivariate normal with mean zero covariance defined by the $n \times n$ R matrix. For all candidate models we assume the observation error variance is constant for all years, the same for each strata and does not co-vary between strata.

$$X_t = Bx_{t-1} + U + w_t, \quad \text{where } w_t \sim \text{MVN}(0, Q_t) \quad (1)$$

$$Y_t = Zx_t + A + v_t, \quad \text{where } v_t \sim \text{MVN}(0, R_t) \quad (2)$$

Candidate models

Candidate models in the a priori determined set were based on previous work on the biology of Pacific cod and more specifically on recently elucidated genetic population structures (?). For all models, $n = 41$, indicating 41 sampled strata within the AIs. The candidate models differ in terms of the number of stocks (m) and which strata belong to which stock. Additionally, within each candidate model we investigated varying levels of complexity. We allowed stock growth rates to be equal or unequal and the process variation to be equal or unequal across stocks and to be independent or correlated by altering the Q matrix. The four hypotheses are:

- **Panmictic** ($m = 1$): all strata are part of a single large panmictic population.
- **EBSvsAI** ($m = 2$): strata are split between the SBS and AI based on the location of Samalga Pass.
- **Amchitka** ($m = 3$): in addition to being split between the SBS and AI, AI strata are split based on the physical location of Amchitka pass.
- **Adak** ($m = 3$): in addition to being split between the SBS and AI, AI strata are split based on the physical location of Adak Strait.

Estimation, uncertainty and model selection

We used the Kalman filter and EM algorithm (?) with 5000 independent runs, to obtain the maximum likelihood (ML) parameters for each candidate model. Confidence intervals (CI) were computed via numerical estimation of the Hessian matrix based on the large-sample properties of ML estimates. To choose the best model of the proposed candidate models we used a version of Akaike's Information Criteria (AIC) corrected designed for small sample sizes (AICc) (?).

Future analyses

Please take note of the following section before reading the remainder of the paper. Models had convergence issues surrounding process error and appear to be degenerate. Prior to publishing this work I plan on obtaining data from the entire Bering Sea and doing one full analysis testing various stock structures based on biology and genetics. I hope more data, with fewer missing years will help convergence issues. In attempt to get models to converge I changed model complexity and tweaked various MARSS control parameters and although the results got better they are still not great. So rather than reporting fake values you will notice some confidence intervals are non-existent.

Results

Stock assessments and subsequently conservation and harvest control rules generated from them, are considered to apply uniformly across individual management areas. There is wide recognition that the delineation of management areas for many marine fish species are inconsistent with biological processes and may lead to violated model assumptions (??), localized depletion or extinctions (?) and the loss of unrealized fishing potential (?). Two types of studies can help inform stock structure: (1) population dynamics analyses to infer biologically based stock structures and (2) genetic analyses to infer migration rates and gene flow. Management based on stock structure inferred from both approaches may be more robust to temporal changes in stock structure and varied patterns of fishing (?).

Consistent with other studies, our analysis rejects the null hypothesis of panmixia, or stock homogeneity, within the BSAI Pacific cod (????), a hypothesis which is also rejected for Atlantic cod *G. morhua* in the northeast Atlantic (???). Results show a definitive stock division at Samalga Pass between AI and SBS Pacific cod, but because the data equally supported three

hypotheses regarding stock structure in the western AIs, it is unclear whether or not western AI Pacific cod population dynamics differ from Pacific cod in the central AIs and/or the SBS.

Assemblages of many species present in the AIs differ to the east and west of Samalga Pass. The pass represents a transition point between colder saltier waters, open-ocean conditions, to the west and warmer fresher waters, coastal conditions, to the east (Figure 4). The two distinct sources of water influence differences in the distribution of nutrients (?) and biota (??) present. Even though Samalga Pass is not particularly deep (200 m), flows through the pass reach $0.4 (10^6 \cdot \text{m}^3 \cdot \text{s}^{-1})$ (?) and can influence the dispersal of pelagic larvae and primary productivity (??), in turn affecting fish diet compositions. East of Samalga Pass diets of Pacific cod are dominated by walleye pollock *Theragra chalcogramma* with small amounts of shrimp, squid and other fishes, whereas west of the pass Atka mackerel *Pleurogrammus monopterygius* become increasingly important along with other prey sources (?). The different water sources for the two areas, Alaskan Coastal Current to the east and the Alaskan Stream to the west, may imply that climate variability could influence the AIs and the SBS in different ways, potentially further increasing differences between Pacific cod stock dynamics in the two areas.

It appears there may also be asynchronous dynamics between Pacific cod located in the eastern and central AIs though our data was unable to confirm this. We tested two separate break points, (1) Amchitka Pass and (2) Adak Strait. Because data were provided as mean CPUE per strata, four strata that spanned the northern side of Amchitka pass had to be removed from all analyses. By removing the strata we were able to create a division at Amchitka Pass rather than to the east or west, while still comparing all models using AICc. The AIC framework rests upon the assumption that the same data be supplied to each model. If spatial locations of each tow were provided, subsequent analyses could include samples from the four removed strata. Including these additional data and documenting the location of each tow would increase the spatial resolution of resulting models and potentially provide more support for a definitive western and central AI Pacific cod stock structure.

Amchitka pass represents one of the deepest passes in the Aleutian chain with depths over 1 000 (m), potentially representing a geographical migration barrier for Pacific cod. Adult Pacific cod can be found at depths up to 500 (m) but are typically found in depths from 80 to 260 (m) (?). Studies of Atlantic cod revealed significant genetic differentiation between all samples separated by wide and deep submarine trenches, suggesting deep ocean features act as barriers to gene flow similar to haddock *Melanogrammus aeglefinus* and other marine species (?). Additionally Logerwell et al. ? found that rockfish community structures show distinct assemblages west and east of Amchitka Pass and differences in growth patterns with smaller size at age in the west. Genetic analyses of Pacific cod show differences in allele frequency west of Amchitka pass and between Great Sitkin and Tanaga Islands, though similar to our results an exact location of a break could not be determined (?).

Whether or not the hypothesized stock structure includes a separation between western and central AI Pacific cod, Pacific cod in the AIs and SBS appear to be growing at the same rate but responding to environmental influences asynchronously. We found support for a single growth rate of less than one across all stocks, which is consistent with the declining biomass estimates for AI and SBS survey areas (?). The 2010 and 2012 estimates of Pacific cod biomass from the AI trawl survey were the lowest measured since the start of the survey in 1980 (?). Support for a single growth rate could indicate (1) equal fishing pressure and net growth rates across all stocks or (2) targeted fishing on stocks with the highest fecundity or lowest natural mortality. The MARSS framework cannot determine the mechanism generating the pattern, only its presence or lack thereof. Elucidating patterns is still a useful exercise, as it may help managers infer which factors are important, where more data should be collected or which mechanisms should be investigated. For example, results from this study highlight a need for determining a possible explanation for increased process error variation in western stocks as compared to eastern stocks. Hypotheses regarding the drivers of differences of year-to-year growth rate variation between stocks would facilitate the addition of covariates to the process error model and potentially reduce the size of confidence intervals around parameter estimates and help model convergence issues.

Given the current management practices of unspecified effort allocation, divergence in estimated population abundances between the AI and the EBS (?) and distinct spatial feeding of Steller sea lions on Pacific cod ?, the question of risk of stock declines should be a topic for future research. Calculating the risk of decline is a natural extension of the MARSS framework. Using simulation the population can be forecasted into the future facilitating the estimation of the probability of decline by a given percentage. A useful metric for managers.

Landings data can provide valuable information on the general distribution and movements of species. The seasonal progression of landings can track general migration patterns, a metric that led to the initial recognition of stocks (??). With time it was recognized that landings data must be standardized to remove the impact of factors other than abundance on changes in catch rates over time. Groundfish surveys, such as those used in this study, can be particularly insightful because all fish are typically identified to species level and catch rates are based on standardized sampling at known sites. Methods to standardize catch rate have developed over time and can account for much more than area trawled, as we did here (?). With missing data in our analysis we were unable to account for potential effects of correlated observation errors across strata within the MARSS framework. Additionally, our method of standardization did not account for the use of different vessels or fundamental differences between US-Japan and US surveys. Both of which could be accounted for using using generalized linear or additive models. Nonetheless, we were able to explicitly account for observation and process error in the analysis providing inferences on how observed trajectories within each strata follow true stock trajectories.

The approach of using MARSS models to measure the synchrony or lack there of between hypothesized stock structures could help managers balance conservation needs on ecological and evolutionary scales at a practical level. Knowing the mechanism behind stock structures and the resiliency of dynamics within each structure is vital to sustainable management decisions. The MARSS framework cannot provide a mechanism but it can provide a tool for managers to establish stock structure at a scale important to them without the need for collecting additional data.

Tables

u	Q	Panamictic.1	SBSvsAI.2	Amchitka.3	Adak.3
same	same	6.7644	4.2190	8.3037	7.2461
same	unique		0.4453	1.4221	0.0000
same	correlated		3.5923	9.4270	9.0455
same	unconstrained		3.5923	9.4270	9.0455
unique	same		6.5321	13.0935	11.9720
unique	unique		2.7062	6.1354	4.7123
unique	correlated		5.7889	14.3054	13.8608
unique	unconstrained		4.7354	7.5881	7.9298

Table 1: Model selection results using Akaike's Information Criteria corrected for small sample sizes (AICc). For each hypothesis the number of stocks is noted after the name. Stock growth rates (u) may be the same or unique and process errors (Q) may be independent and identical (same), independent and unequal (unique), unequal with a single covariance (correlated) or unequal with unconstrained covariance (unconstrained). The model with the most support from the data defines three stocks, where the stocks are divided by Adak Strait and Samalga Pass, share a similar growth rate and have different process error variance but zero covariance. Model selection results are reported as delta AICc values in relation to the model with the highest support (best model)

Adak	SVSvsAI	Amchitka
6.524 (5.119-8.315)	6.846 (5.353-8.756)	6.499 (5.099-8.284)
0.966 (0.94-0.993)	0.966 (0.936-0.997)	0.967 (0.94-0.996)
1.234 (0.992-1.536)	1.095 (0.992-1.208)	1.272 (0.985-1.642)
1.017 (0.973-1.063)	NA	1.029 (0.972-1.091)
1 (NA-NA)	1 (NA-NA)	1 (NA-NA)
857.405 (249.227-2949.689)	1264.877 (681.333-2348.211)	894.322 (232.483-3440.302)
669.34 (287.972-1555.763)	654.18 (251.618-1700.796)	2888.403 (608.923-13701.026)
651.318 (260.545-1628.18)	NA	635.745 (250.05-1616.367)

Table 2: Maximum likelihood estimates for the three models with delta AICc less than 2.0. Means are given with 95 percent confidence intervals in parantheses. A value of NA indicates the parameter was not included in that particular model and a confidence interval of NA indicates the parameter estimate did not converge for that model. Lack of convergence will be dealt with in subsequent analyses before publication.

Figures

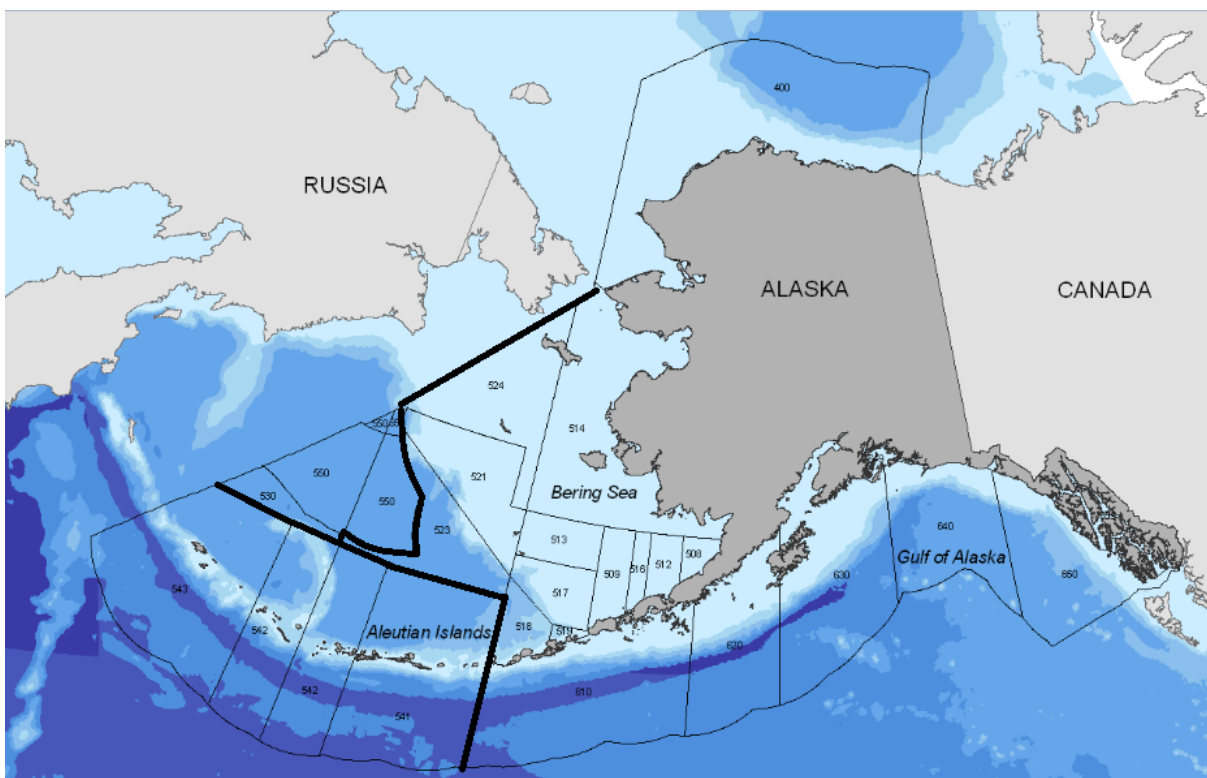


Figure 1: Map of Alaska delineating the regulatory areas of the North Pacific Fishery Management Council (NPFMC) and their corresponding statistical areas. The statistical areas 541, 542, 543 and 518 are referred to by the NPFMC as the eastern, central and western Aleutian Islands (AI) and southern Bering Sea (SBS) respectively.

References

- Bakkala, R. 1984. Pacific cod of the eastern Bering Sea. *International North Pacific Fisheries Commission Bulletin* **42**: 157–179
- Begg, G. A., Friedland, K. D. and Pearce, J. B. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. *Fisheries Research* **43**(13): 1–8. doi: 10.1016/S0165-7836(99)00062-4
- Begg, G. A. and Waldman, J. R. 1999. An holistic approach to fish stock identification. *Fisheries Research* **43**(1): 3544
- Bentzen, P., Taggart, C. T., Ruzzante, D. E. and Cook, D. 1996. Microsatellite polymorphism and the population structure of Atlantic cod (*Gadus morhua*) in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(12): 2706–2721. doi:10.1139/f96-238
- Booth, A. 2000. Incorporating the spatial component of fisheries data into stock assessment models. *ICES Journal of Marine Science* **57**(4): 858–865. doi:10.1006/jmsc.2000.0816

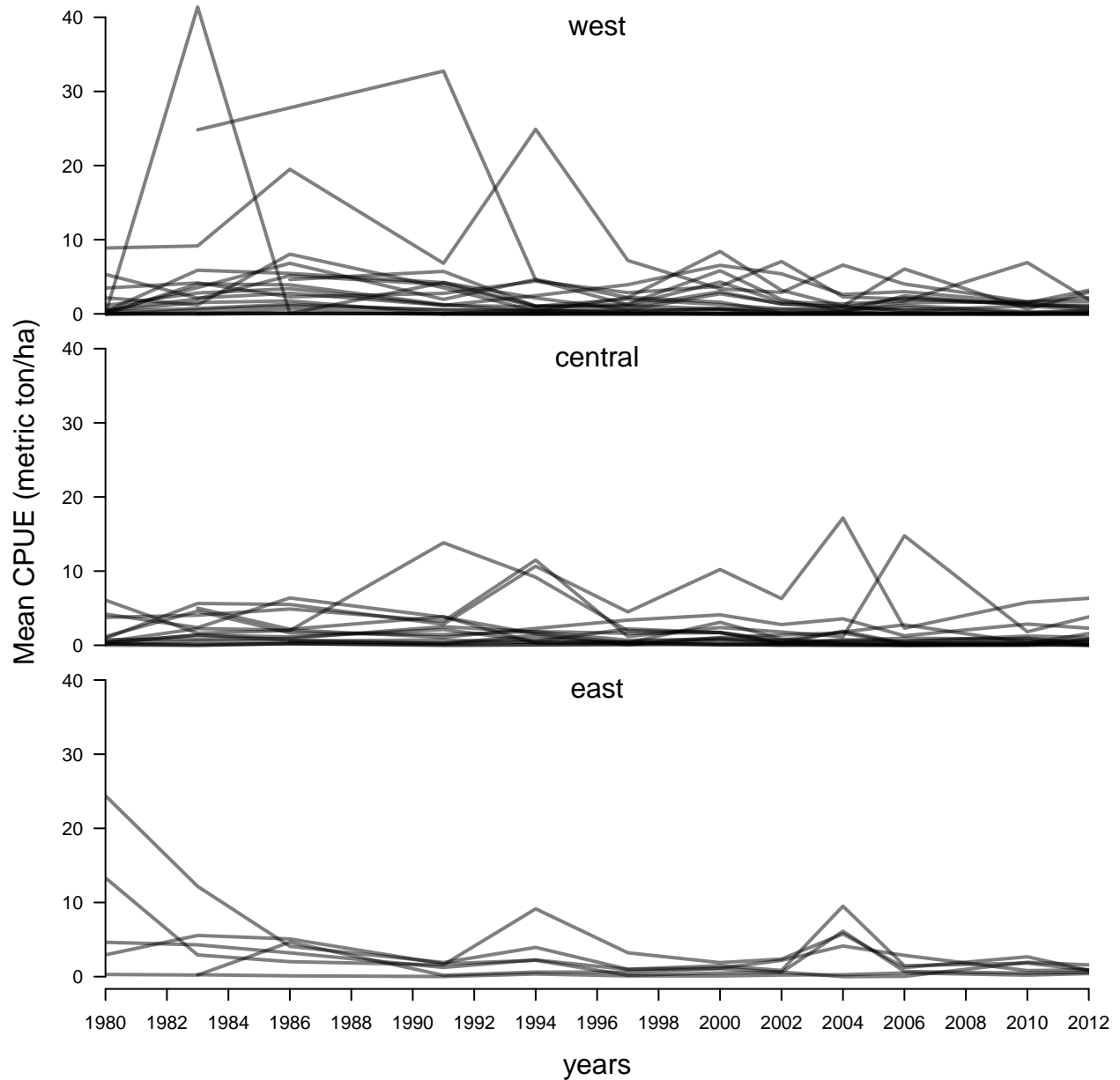


Figure 2: Mean catch per unit effort (CPUE) (metric ton per hectare) for each of the 41 strata. Missing data are interpolated between sampled years and lines appear darker where the mean CPUE was similar across strata. Strata trajectories are grouped according to results from the best model, with western strata divided from central strata at Adak Pass and central strata divided from the southern Bering Sea at Samalga Pass.

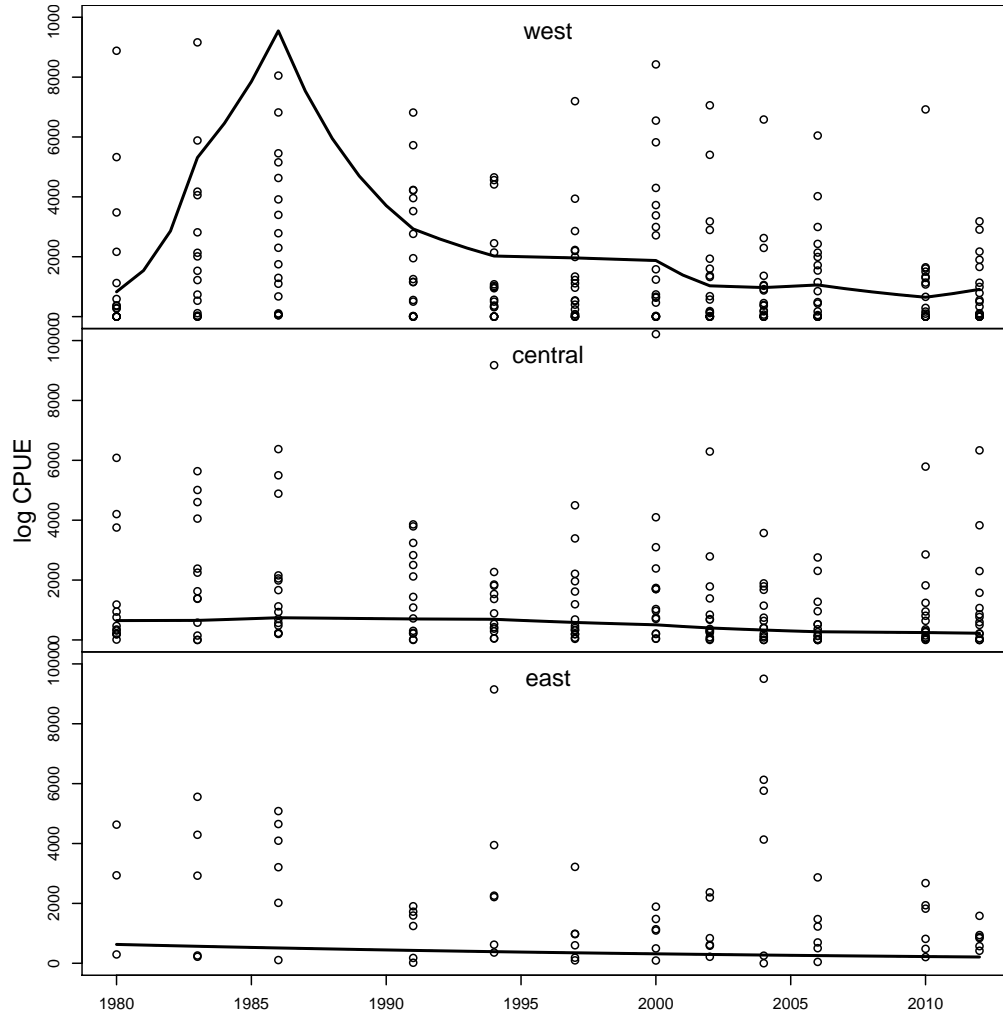


Figure 3: Fits of the best model, where stocks are differentiated by Adak Pass and Samalga Pass. Maximum likelihood estimates of the state trajectories, or stocks (solid line), are conditioned on the entire dataset. Data from each of the 41 strata (circles) are grouped by stock according to the best model. Confidence intervals (95%) should be displayed with dashed lines, though the models were somewhat degenerate and experienced difficulty fitting process error. This will be dealt with prior to publication.

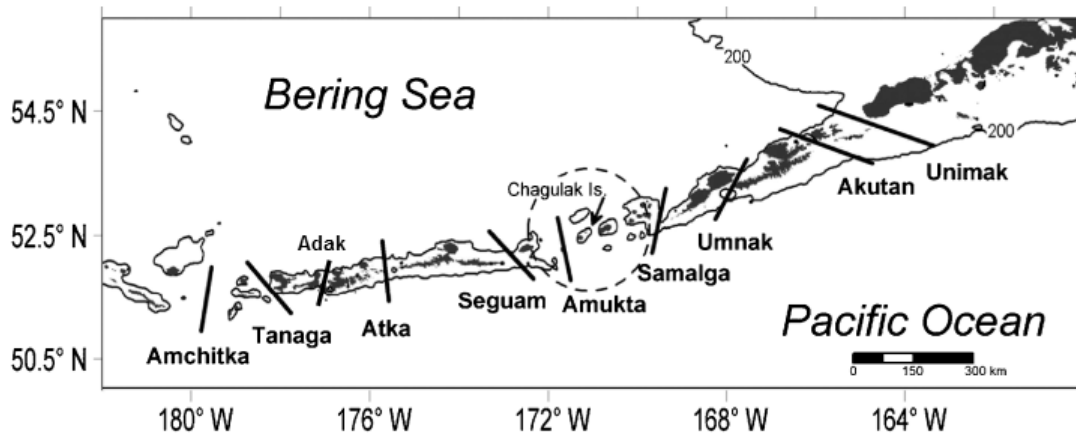


Figure 4: Major passes separating the Bering Sea from the Pacific Ocean along the Aleutian Islands. Flows to the west of Samalga Pass are dominated by the Alaskan Stream compared to west of the pass where the Alaskan Coastal Current is the dominate source of nutrients.

- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer
- Canino, M. F., Spies, I. B., Cunningham, K. M., Hauser, L. and Grant, W. S. 2010. Multiple ice-age refugia in Pacific cod, *Gadus macrocephalus*. *Molecular Ecology* **19**(19): 4339–4351. doi:10.1111/j.1365-294X.2010.04815.x
- Canino, M. F., Spies, I. B. and Hauser, L. 2005. Development and characterization of novel di- and tetranucleotide microsatellite markers in Pacific cod (*Gadus macrocephalus*). *Molecular Ecology Notes* **5**(4): 908–910. doi:10.1111/j.1471-8286.2005.01109.x
- Casselman, J. M., Collins, J. J., Grossman, E. J., Ihssen, P. E. and Spangler, G. R. 1981. Lake whitefish (*Coregonus clupeaformis*) stocks of the Ontario waters of Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences* **38**(12): 1772-1789
- Cope, J. M. and Punt, A. E. 2008. Drawing the lines: resolving fishery management units with simple fisheries data. *Canadian Journal of Fisheries and Aquatic Sciences* **66**(8): 1256–1273. doi:10.1139/F09-084
- Coyle, K. O. 2005. Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. *Fisheries Oceanography* **14**: 7792. doi:10.1111/j.1365-2419.2005.00367.x
- Cunningham, K. M., Canino, M. F., Spies, I. B. and Hauser, L. 2009. Genetic isolation by distance and localized fjord population structure in Pacific cod (*Gadus macrocephalus*): limited effective dispersal in the northeastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* **66**(1): 153–166. doi:10.1139/F08-199
- Ford, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. *Journal of the Marine Biological Association of the United Kingdom (New Series)* **19**(01): 305-384
- Grant, W. S., Zhang, C. I., Kobayashi, T. and Sthl, G. 1987. Lack of Genetic Stock Discretion in Pacific Cod (*Gadus macrocephalus*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**(3): 490–498. doi:10.1139/f87-061

- Hart, J. L. 1973. Pacific fishes of Canada. *Fisheries Research Board of Canada*(Bull. 180), Ottawa, Canada. 749 1973
- Hilborn, R., Quinn, T. P., Schindler, D. E. and Rogers, D. E. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences* **100**(11): 6564-6568
- Hinrichsen, R. and Holmes, E. E. 2009. Using multivariate state-space models to study spatial structure and dynamics. In R. S. Cantrell, R. Cosner and S. Ruan, eds., *Spatial Ecology*, 145–166. CRC/Chapman Hall, Boca Raton, FL
- Hobson, K. A., Sease, J. L., Merrick, R. L. and Piatt, J. F. 2006. Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Marine Mammal Science* **13**(1): 114-132
- Holmes, E. E., Ward, E. J. and Wills, K. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *The R Journal* **4**(1): 30
- Hutchings, J. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(5): 943–962. doi:10.1139/cjfas-53-5-943
- Jahncke, J., Coyle, K. O. and Hunt, G. L. 2005. Seabird distribution, abundance and diets in the eastern and central Aleutian Islands. *Fisheries Oceanography* **14**: 1601-77. doi:10.1111/j.1365-2419.2005.00372.x
- Lockwood, S. J. 1988. The mackerel: its biology, assessment and the management of a fishery. Fishing News Books
- Logerwell, E. A., Aydin, K., Barbeaux, S., Brown, E., Conners, M. E., Lowe, S., Orr, J. W., Ortiz, I., Reuter, R. and Spencer, P. 2005. Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. *Fisheries Oceanography* **14**: 931-12. doi:10.1111/j.1365-2419.2005.00366.x
- Maunder, M. N. and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* **70**(23): 141–159. doi:10.1016/j.fishres.2004.08.002
- Mordy, C. W., Staben, P. J., Ladd, C., Zeeman, S., Wisegarver, D. P., Salo, S. A. and Hunt, G. L. 2005. Nutrients and primary production along the eastern Aleutian Island Archipelago. *Fisheries Oceanography* **14**: 557-6. doi:10.1111/j.1365-2419.2005.00364.x
- Pawson, M. G. and Jennings, S. 1996. A critique of methods for stock identification in marine capture fisheries. *Fisheries Research* **25**(34): 203–217. doi:10.1016/0165-7836(95)00441-6
- Porch, C. and Scott, G. 1993. A numerical evaluation of GLM methods for estimating indices of abundance from west Atlantic bluefin tuna catch per trip data when a high proportion of the trips are unsuccessful. Tech. Rep. SCRS/93/75, ICCAT Working Document SCRS93/75
- Rothschild, B. J. 2007. Coherence of Atlantic Cod Stock Dynamics in the Northwest Atlantic Ocean. *Transactions of the American Fisheries Society* **136**(3): 858–874. doi:10.1577/T06-213.1
- Ruzzante, D. E., Taggart, C. T. and Cook, D. 1998. A nuclear DNA basis for shelf- and bank-scale population structure in northwest Atlantic cod (*Gadus morhua*): Labrador to Georges Bank. *Molecular Ecology* **7**(12): 1663–1680. doi:10.1046/j.1365-294x.1998.00497.x
- Seijo, J. C., Prez, E. P. and Caddy, J. F. 2004. A simple approach for dealing with dynamics and uncertainty in fisheries with heterogeneous resource and effort distribution. *Marine and Freshwater Research* **55**(3): 249–256

- Shimada, A. M. and Kimura, D. K. 1994. Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data. *Fishery Bulletin* **92**(4): 800816
- Shumway, R. H. and Stoffer, D. S. 2011. State-Space Models. In Time series analysis and its applications: with R examples, Springer texts in statistics, 319–404. Springer, New York, 3rd ed ed.
- Sinclair, E. H. and Zeppelin, T. K. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy* **83**(4): 973–990
- Spies, I. 2012. Landscape Genetics Reveals Population Subdivision in Bering Sea and Aleutian Islands Pacific Cod. *Transactions of the American Fisheries Society* **141**(6): 1557–1573. doi: 10.1080/00028487.2012.711265
- Springer, A. M., Piatt, J. F. and Vliet, G. V. 1996. Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc. *Fisheries Oceanography* **5**(1): 45–55. doi:10.1111/j.1365-2419.1996.tb00016.x
- Stauffer, G. 2004. NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. Tech. rep., U.S.D.O.C., NOAA Tech Memo, NMFS-SPO-65
- Thompson, G. G. and Lauth, R. R. 2012. Assessment of the Pacific Cod Stock in the Eastern Bering Sea and Aleutian Islands Area. Tech. rep., NOAA NMFS AFSC, Seattle
- von Szalay, P. G., Rooper, C. N., Raring, N. W. and Martin, M. H. 2011. Data Report: 2010 Aleutian Islands bottom trawl survey. Tech. Memo NMFS-AFS-215, U.S.D.O.C., NOAA Tech. Memo. NMFS-AFSC-215
- Waldman, J. R. 1999. The importance of comparative studies in stock analysis. *Fisheries Research* **43**(1-3): 237–246. doi:10.1016/S0165-7836(99)00075-2
- Waples, R. S. and Gaggiotti, O. 2006. INVITED REVIEW: What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular ecology* **15**(6): 14191439