Using gradients in productivity to inform stock structure: a case study for Pacific cod in Alaska

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# Abstract

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# Keywords

Aleutian Islands, Alaska, Gulf of Alaska, Gompertz model, Pacific cod, random field, stock structure

# Introduction

The first step in the management of natural resources is to determine the management unit, which will depend on the management objectives. Unfortunately, management objectives are not static, therefore it follows that management units should evolve in tandem with changing management objectives (Begg and Waldman, 1999; Reiss *et al.*, 2009). Furthermore, environments are not 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 default, often political, and biological stock boundaries.

Management objectives for commercially fished marine species typically prioritize optimizing long-term sustainable yields, while conserving biological characteristics that facilitate such optimal yields (Hilborn and Walters, 1992; Punt *et al*., 2006). To achieve the previous, fisheries managers must design, politically justify, and implement restraints on fishing activities. Output from stock assessment models provides scientific advice to fisheries managers regarding the current status of the management unit (stock) and how it may potentially respond to future management measures. A major assumption of stock assessment models is that fish within the stock are homogeneous (i.e., similar growth, natural mortality, risk of fishing, etc.) (Waldman, 2005; Rothschild and Jiao, 2011). Thus, geographic boundaries of fish stocks should be defined using a method based on population dynamics (life-history) parameters (Carvalho and Hauser, 1995; Begg and Waldman, 1999; Quinn and Deriso, 1999) (Cope & Punt 2009).

Life-history parameters (growth, survival, age-at-maturation, fecundity, distribution, and abundance) are influenced by the specific biotic and abiotic environment inhabited by a stock due to their sensitivity to both environmental and anthropocentric influences (Begg *et al*., 1999). Furthermore, even though life-history parameters do not provide direct information about the genetic composition of the stock, phenotypic variation results from the interaction between genotypes and their environment, thus providing a proxy for genetic structure (Campana *et al*., 1995). In short, using easy to measure life-history data to delineate stock boundaries can provide a good starting point for more advanced stock identification techniques (e.g. behavioural, biochemical, cytogenetics, immunological, meristic, morphometric, parasitic, protein electrophoresis, scale morphology, otoliths, serological, stable isotopes, tag-recovery, etc.), while being cost effective and efficient (Begg *et al*., 1999; Smedbol and Stephenson, 2001).

Almost all fish species exhibit complex spatial structure in their population dynamics (Conover *et al*., 2006; Cope and Punt, 2009). Consequently, understanding stock structure becomes increasingly important when stocks of a given species are differentially exploited (Altukhov, 1981; Ricker, 1981). Fisheries that reduce stocks to low levels for extended periods of time can lead to reduced genetic diversity, which can ultimately lead to lowered adaptability, population productivity, and persistence (Lacy, 1987; Lande, 1993; Hauser *et al*., 2002). Matching stocks with biological units helps minimize the risk of depleting distinct stocks (Frank and Brickman, 2000; Laikre *et al*., 2005; Sterner, 2007) and helps maintain stable stock complexes (Schindler, 2010).

Currently, no single method, whether it be based on life-history parameters, genetics, otolith structure, parasitic composition, etc., properly identifies all stocks. Several 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) can be advantageous. Unfortunately, proper intepretation of fisheries data requires account for both observation and process error, which can complicate analyses.

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) (Millar & Meyer 2000) and later extended into two-dimensional space for movement data (Jonsen, Myers, and Flemming, 2003) and multiple subpopulations (Ward *et al*., 2010) and species (Mattsson *et al*., 2013). Multivariate time-series analysis is one way to detect patterns of correlation and synchrony across multiple scales (Ward *et al*., 2010) and can provide inferences on stock structure based on ecological differences across stocks. Unfortunately these models rely on the user to specify hypothesized stock structures (i.e., manually grouping the data according to hypothesized stock structures). Additionally, parameter estimates from non-spatial population models may be biased when density or productivity varies spatially (Thorson *et al*., In press), making it necessary to explicitly include space. Accounting for space can be accomplished by replacing relevant, scalar, life-history parameters with spatial or spatio-temporal random effects (Cressie and Wikle, 2011; Gelman *et al*., 2013). Subsequently, spatially-explicit estimates of productivity can be used to help inform stock structure.

Here we quantify spatial differences in productivity for Pacific cod (*Gadus macrocephalus*; hereafter referred to as cod) in the north east Pacific Ocean using spatially-explicit Gompertz population dynamics models, implemented within a state-space formulation (Thorson et al. In press). Cod is both an ecologically and commercially important species in the Bering Sea Aleutian Island and Gulf of Alaska (GOA) large marine ecosystems. Cod represents the second largest fisheries by weight in all of Alaska (329,040 (t); st.nmfs.noaa.gov). Furthmore, cod is one of the five most common prey species (frequency of occurrence in diet data (FO) 16.1%) of the federally endangered Steller sea lion (*Eumetopias jubatus*; SSL) (Sinclair and Zeppelin, 2002). The method should be useful to researchers looking to inform stock structures of species for which fisheries-independent data exists yet precise structures remain unclear.

# Materials and methods

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## Spatial fields

Spatial data were defined as realizations of a stochastic process indexed by space

, Eq. 1

where the domain, Ɗ, is a fixed subset of ℝd (here d = 2) and the set, *s* , indicates the spatial units at which the measurements were taken. The data were point-referenced nonzero *CPUE* measurements of a continuous random process, modelled using the stochastic partial differential equation (SPDE) approach proposed by Lindgren *et al*. (2011). SPDEs use sparse inverse-covariance matrices, which facilitate modeling space as a continuous process without the “big *n* problem” (Jona-Lasinio *et al*., 2012; *et al*., 2012; Banerjee *et al*., 2004) caused by dense inverse-covariance matrices.

Assuming that

, Eq. 2

where is the variance of the mean measurement error, or nugget effect, and is the mean response

, Eq. 3

where is the large-scale component composed of an intercept, , and coefficients , which quantify the effects of the measured covariates , and is the realization of the latent Gausian Random Field (GRF), it follows that is independent of when .

Triangulation of Ɗ facilitates the transformation of the GRF to a discretely-indexed Gaussian Markov random field (GMRF)

, Eq. 4

where *G* is the total number of vertices in the triangulation, { is the set of basis functions, and are the non-zero distributed weights. Basis functions were chosen such that was 1 at vertex *g* and 0 everywhere else (Lindgren *et al*., 2011). GMRFs are characterized by a multivariate Normal distribution with mean **μ** = (μ­1, …, μn)′ and a spatially-structured covariance matrix Σ, whose generic element is defined as

Σi,j = Cov(θi, θj) = . Eq. 5

Here, is the variance component for and is the (isotropic) Matérn spatial covariance function (Cressie, 1993), which depends on the Euclidean distance between the locations . A GF with a Matérn covariance function

, Eq. 6

provides an exact solution to the SPDE, which can be approximated using a finite element representation (Eq. 4). Here, is the modified Bessel function of second kind and order (here ) measuring the degree of smoothness. The range (),

, Eq. 7

was defined as the distance at which the spatial correlation is approximately 0.1, using κ>0 as a scaling parameter, according to Lindgren *et al*. (2011; see Section 2).

## Gompertz model

Population dynamics were modelled using a spatial equivalent of the Gompertz model (Thorson *et al*. In press). The Gompertz model has been used extensively in applied and theoretical investigations …., and the spatial Gompertz model specifies per-capita productivity as a log-linear function of local density,

, Eq. 8

where is the density at all spatial locations [x,y] in year *t*, ρ is the strength of density dependence (define interpretations), Ω is the intercept represented by a GMRF

Ω ~ *MVN*(α**1**, ΣΩ) Eq.

where α**1** is a vector and α is the mean productivity of the GMRF, and is a GMRF

Εt ~ *MVN*(0, ΣΕ) Eq. 10

representing the spatial variation in process error in year *t*. ΣΩ and ΣΕ­ are defined as above (Eq. 5) with independent marginal variance components ( and respectively) but equal Matérn spatial covariance functions.

The model has a stationary distribution

Eq. 11

when . Initial conditions, representing the population when *t*=1, were specified using the following equation:

, Eq. 12

where ϕ**1** is the log-ratio of expected abundance in the initial year (*t*=1) and the median of the stationary distribution for abundance at equilibrium. is are statistically-independent of conditional on a fixed value for .

## Estimation procedure

Data were assumed to follow a lognormal distribution

, Eq. 13

where, is the predicted density at a given vertex *i* located at the points [*x*, y] on the triangulation mesh (Fig. 2), is the standard deviation of the observation error, and are the *CPUE* observations located in the triangulation vertex *i* in year *t*.

GMRF matrices were computed using functions available in the INLA package (Rue *et al*., 2014; Illian *et al*., 2012) implemented in the R statistical software environment (R Core Team, 2014). A single triangulation network (Fig. 2), created via the *inla.mesh.2d* function, was used to facilitate the comparisons across species. Nodes for the triangulation network were specified using locations of the raw data, with nodes added and removed according to arguments controlling the tradeoff between variance and precision. Subsequently, INLA was used to calculate the precision matrix of the GMRF

Eq. 14

The three sparse precision matrices ( were then passed to Template Model Builder (TMB) (Kristensen *et al*., 2013), the software program used for parameter estimation. TMB uses the integrated nested Laplace approximation (Skaug and Fournier, 2006) to calculate the marginal likelihood of the fixed-effect parameters integrated across all random fields, while also calculating the gradient of the marginal likelihood via automatic differentiation. Fixed effects were then subsequently optimized using traditional tools in R by maximizing the log-marginal likelihood. Confidence intervals were calculated using the delta-method (see Thorson *et al.* In press for alternative estimation methods).

The triangulation mesh used to model spatially explicit Gompertz population dynamics had 185 vertices with vertices located closer in space where the density of non-zero CPUE measurements was higher (Fig. 2). The same triangulation mesh was used for all years, even though fisheries-independent surveys were never conducted across the entire study area in a single year. The GOA and the AIs were typically sampled in odd and even years respectively (Fig. 3). On average, the yearly mean CPUE was higher in the GOA compared to the AIs, but an increased number of non-zero CPUE measurements were consistently collected in the AIs compared to the GOA (Fig. 3).

## Stock boundaries

Stock delineations were based on a partitioning routine that recursively partitioned the data into successively smaller groups with binary splits based on a single predictor variable, known as a Regression Tree (RT). Splits for predictor variables were examined using an exhaustive search procedure until the best splits were found, defined as values of the predictor variable that maximize the homogeneity of the two resulting groups with respect to the response variable (i.e., maximizing the between-group sum of squares, as in an analysis of variance). Once the best splits were found, RTs were pruned to collapse the weakest links by minimizing the cross-validated error (Hastie *et al*., 2001). Here, the response variable was Ω and the predictor was longitude. Analyses were performed using the rpart package (Therneau *et al*., 2014) implemented in R.

# Results

Density dependence was estimated as compensatory, although the strength of ρ was relatively weak (0.703, se = 0.108; Fig. 4). Current biomass estimates for the entire study area are far less than the theoretical equilibrium biomass, with the initial biomass (*t*=1) estimated at approximately 20% of its equilibrium potential (Fig. 4). Productivity was relatively lower in the GOA than the AIs, with the highest productivity estimated in the far reaches of the AIs (Fig. 5). Productivity was also relatively high near Unimak and Samalga Passes (Fig. 5).

Partitioning algorithms grouped cod into two distinct stocks based on 152° 15' 24.463" W (Figs. 5 and 6). Further potential stock boundaries were noted at 178° 35' 0.679"W, 158° 59' 12.633" W, and 170° 41' 9.642" W, although none of the splits significantly improved the cross validated error enough to warrant their inclusion in the final stock structure.

# [Sentence regarding differences in trend for 2 proposed stocks, Fig. 4 – this is exciting because they seem to have different trends!] [maybe a sentence/figure comparing these trends with trends arising with more splits – only if you feel like you want to bulk up your results section, which I personally don’t think is strictly necessary]Discussion

Todo: Write discussion

# Acknowledgements

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# Tables

Todo: result tables

Table

# Figures

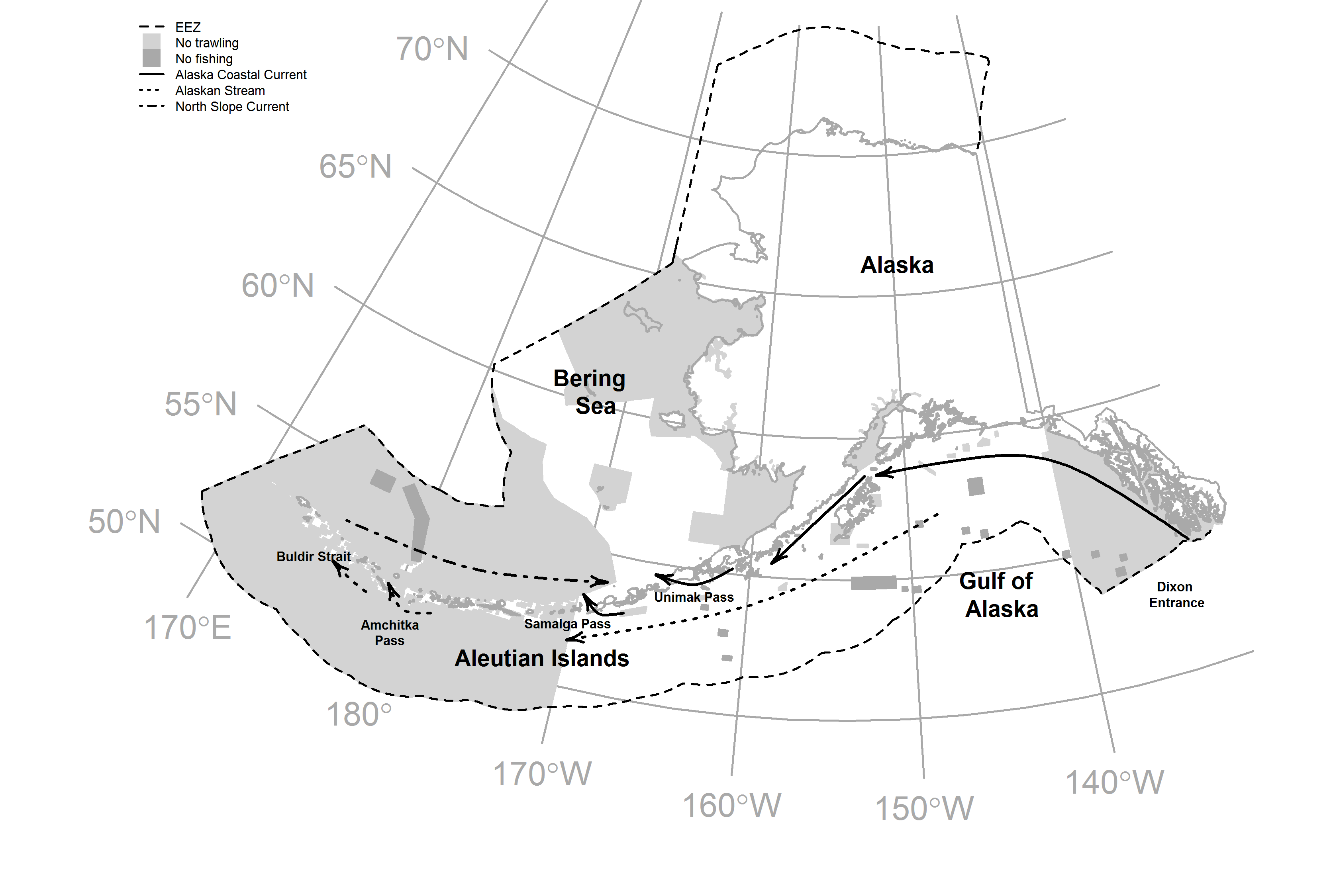


Figure 1. Map of the study area with major currents. Dashed line marks the United States Exclusive Economic Zone (EEZ). Dark gray polygons are areas with no fishing and light gray polygons are areas with no trawling. The light gray polygon near Dixon Entrance demarks the Southeast Alaska Outside Trawl Closure.

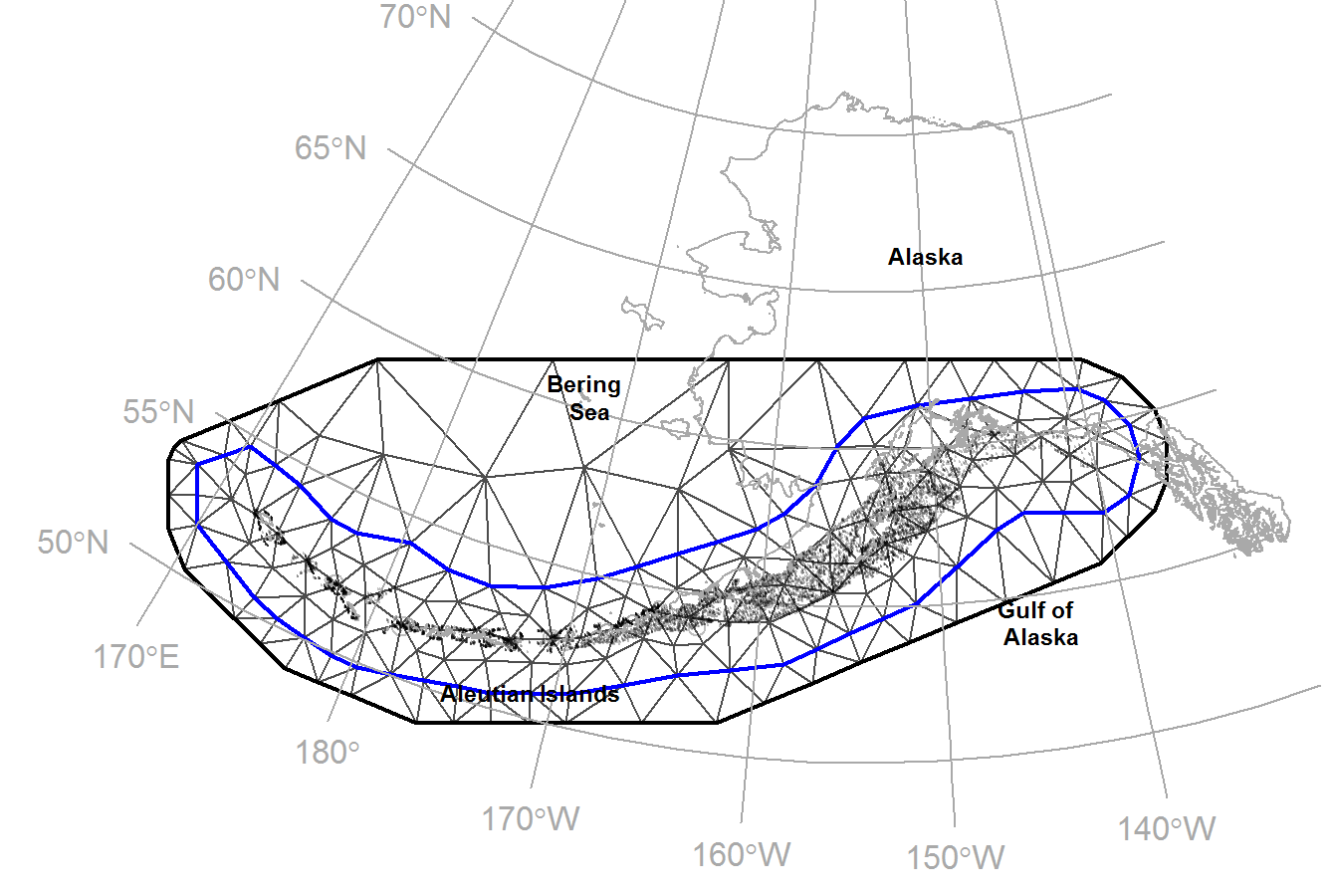


Figure 2. Catch per unit effort (CPUE, kg ha-1) for Pacific cod for all years (1990-2013). Point size is proportional to the maximum observed CPUE and points are shown with transparency to depict areas with higher sampling effort. Black lines display the triangulation matrix used to approximate a continuous Gaussian Random Field (GRF) using a Gaussian Markov Random Field (GMRF). The blue line represents the border defining the “inner” more precise nodes, while the thick black line represents the “outer” border defining the boundary.

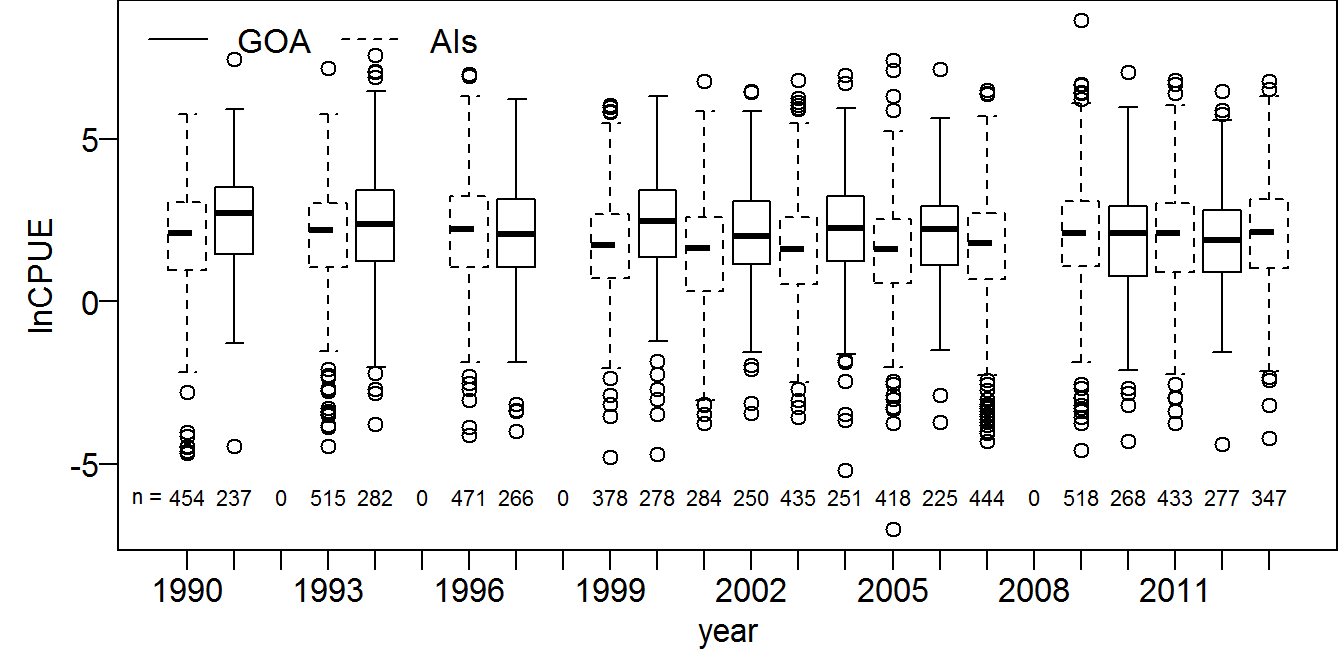


Figure 3. Yearly variation in non-zero catch per unit effort (CPUE, kg ha-1) measurements on the natural log scale for Pacific cod between stations sampled in the Gulf of Alaska (solid lines) and Aleutian Islands (dashed line).

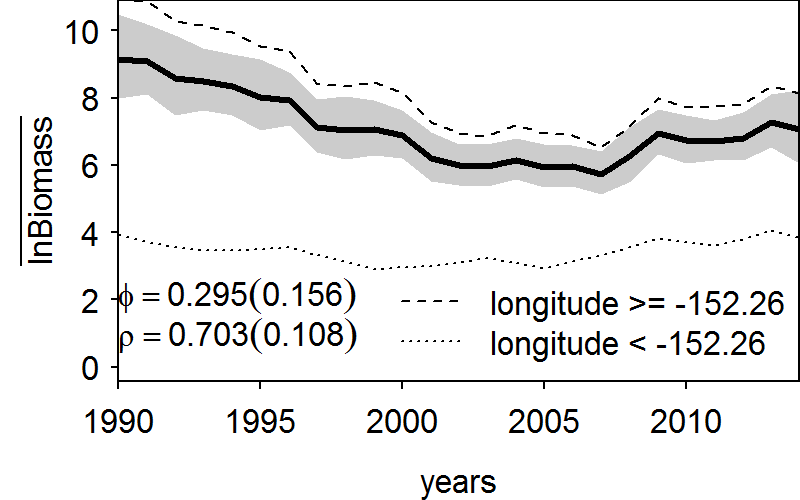


Figure 4. Estimated mean natural log biomass for the entire study area (i.e., Aleutian Islands and the Gulf of Alaska). Parameter estimates along with their standard errors, in parentheses, are given for i) density dependence (ρ) and ii) the log-ratio of expected abundance in the initial year (*t*=1) and the median of the stationary distribution for abundance at equilibrium (ϕ). Dashed lines display the mean log biomass for each hypothesized stock.

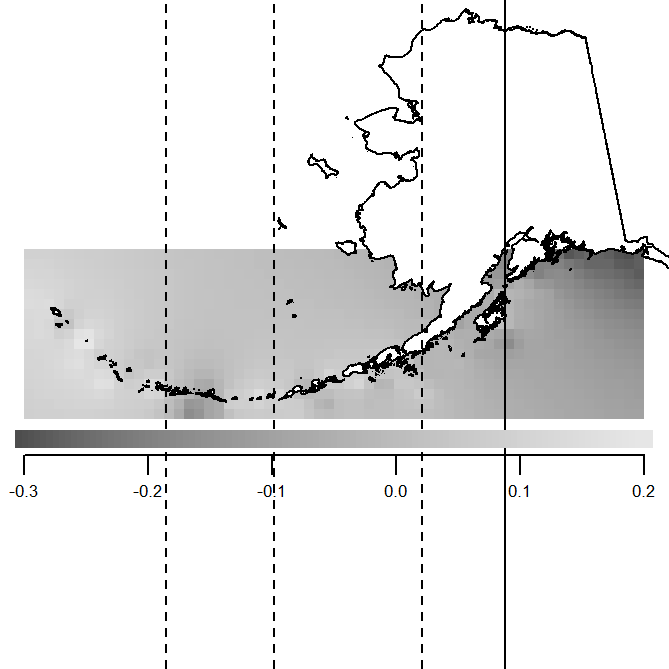


Figure 5. Spatial variation in productivity (EΩ) displayed using inverse distance weighting, where colors are proportional to the estimated value. Vertical solid line demarks hypothesized stock boundary and vertical dashed lines demark hypothesized stocks which were pruned from the final regression tree.

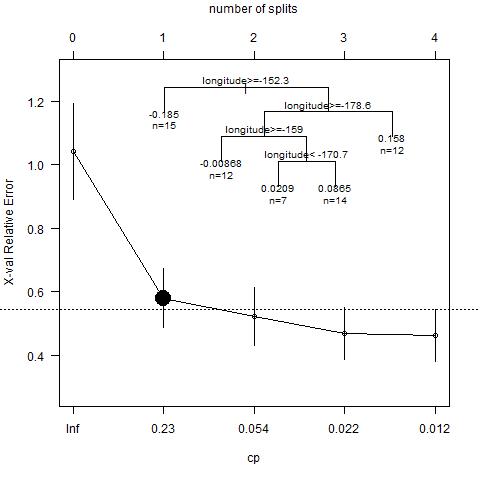


Figure 6. Cross validated relative error versus a complexity parameter (cp) to determine optimal pruning, where splits define distinct stock boundaries. The large black dot represents the best number of splits, with the location of each split displayed in the upper left inset. Regression trees worked to partition the variation (minimize the within group variation) in ΣΩ across a longitudinal gradient.