Using gradients in productivity to inform population structure for a managed species: a case study for Pacific cod in Alaska

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# Abstract

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# Keywords

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# 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 and 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 interpretation of fisheries data requires accounting 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 (Millar and Meyer, 2000; 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*., 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 dependence 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; 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

## 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 measure covariates , and is the realization of the latent Gaussian 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 GRF 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 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, 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 statistically-independent of , conditional on a fixed value for .

## Study area

The study area included the Aleutian Islands (AIs; 170° E to 170° W), a portion of the Southern Bering Sea (BS) (165° W to 170° W along the north side of the AIs), and the GOA (132°40’ W to 170° W) (Figure 1). The AIs are an extensive archipelago comprised of 14 large and hundreds of small volcanic islands, characterized by a relatively narrow continental shelf, crossed by numerous deep passes. Conversely, the GOA is characterized by a semi-enclosed basin, with a relatively shallow shelf that varies in width from 5 km in the southeast to more than 200 km in the north.

## Data

Survey data were collected by the Alaska Fisheries Science Center of the National Marine Fisheries Service from 1982 to 2014 during the triennial GOA and AIs bottom trawl surveys. These data are used to provide estimates of absolute or relative abundance (A’mar *et al*., 2013; Aydin *et al*., 2013), define distributions, and inform biological parameters of groundfish and crab to the North Pacific Fishery Management Council (NPFMC).

Surveys employed a stratified random sampling design, with grids determined by NPFMC regulatory areas, which were further divided into depth strata. The AI surveys covered depths up to 500 m along the north side of the AIs from Unimak Pass (165° W) westward to Samalga Pass (170° W) and on both sides of the AIs from Samalga Pass to Stalemate Bank (170° E) (von Szalay *et al*., 2011). The GOA survey covered depths up to 1000 *m* from Samalga Pass to Dixon Entrance (54°30’ N, 132°40’ W) (Raring *et al*., 2011). Surveys in the AIs were conducted in 1983, 1986, 1991, 1994, 1997, 2000, 2002, 2004, 2006, 2010, 2012, and 2014. Surveys in the GOA were conducted in 1984, 1987, 1990, 1993, 1996, 1999, 2001, 2003, 2005, 2007, 2009, 2011, and 2013. The analysis was restricted to data collected after 1989 and east of 140° W because of the lack of standardized gear and effort measurements prior to 1990 (Munro and Hoff, 1995) and because of the Southeast Alaska Outside Trawl Closure, respectively (Figure 1).

Tows of 15 min (estimated on-bottom duration) at speeds of 3 knots were conducted at each sampled station. For each tow, species composition of the catch was determined and species-specific catch per unit effort (*CPUE*) was calculated as the weight of the catch (kg) divided by the area swept (ha) for a given trawl (Figure 2). Global positioning (GPS) locations for each trawl were projected using the Albers equal-area conic projection, an equal area map projection.

## 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 mesh (Fig. 2), is the standard deviation of the observation error, and are the *CPUE* observations located in the vertex *i* in year *t*. was of positive length, including zero, where missing data occurred one of two ways: i) no observations at vertex *i* for year *t*, or ii) no trawl was conducted at 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).

## 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

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).

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 greater than the theoretical equilibrium biomass, with the initial biomass (*t*=1) estimated at approximately 134% 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!
* Sentence/figure comparing these trends with trends arising with more splits – only if you feel like you want to bulk up your results section
* Estimates of process error

# Discussion

The majority of stock assessment models assume data comes from a single stock, thus life-history characteristics that characterize the population demographics of a stock should be homogeneous across space. Yet here, a spatially explicit Gompertz population dynamics model provides support for rejecting the hypothesis that cod exhibit homogeneous life-history characteristics throughout the GOA. More specifically, local estimates of productivity vary with longitude, leading to patches of high and low productivity within the study area (GOA and AIs) that do not align with current management measures.

Using quantitative analyses to test hypotheses regarding synchrony in population dynamics between multiple datasets (i.e., sampling locations or species) is not new (Moran, 1953; Ives *et* al., 2003). Methods range from simple analyses of correlation between datasets (Casselman *et al*., 1981) to using complex state-space models that explicitly account for both process and environmental error along with model selection (e.g. Akaike information criteria) to determine the relative support for various grouping structures (Ward *et al*., 2010; Flesch, 2014). A potential problem with these approaches is that as the number of time-series increases, the number of testable hypothesis exponentially increases and it assumes the *a priori* determined set of hypotheses includes the correct hypothesis prior to exploring the data (Cook and Campbell, 1979). In this study we alleviate this problem by fitting a single model, the spatial Gompertz model, which replaces traditional scalar functions (productivity and process error) with random fields, followed by algorithmic methods to discover the relationship between space and productivity. Thus, this approach potentially allows non-omniscient observers to discover relationships that may be hidden or previously not thought of.

Identifying spatial variation in life-history characteristics does not reveal the biological mechanisms or environmental factors leading to the patterns, but it can provide inference to potentially important drivers of the variation and which factors should be studied. The separation of stocks here seems to be linked to oceanographic features in the study area.

* Oceanography of AI and GOA
* Tagging studies (e.g., Shimada and Kimura 1994) have demonstrated significant migration both within and between the EBS, AI, and Gulf of Alaska (GOA). Migration does not always mean similar population dynamics.
* Increasing the use of spatial models, such as the one used here, may increase scientists ability to understand ecological processes, such as population dynamics, which are deeply dependent on space (Legendre, 1993; Kareiva *et al*., 1990).
* Similarity to atlantic cod
* Current management
  + discrete stocks in the EBS and AI (Canino et al. 2005, Cunningham et al. 2009, Canino et al. 2010, Spies 2012).
  + Until relatively recently (2013) cod was managed as just two stocks in Alaska, the Bering Sea Aleutian Island and GOA. Currently, cod in Alaska is managed as three stocks: i) Bering Sea (not included in this study), ii) AIs, and iii) GOA. The historical stock boundary, used by the NPFMC, to delineate between the AI and GOA stocks of 170° W does not align with the stock boundary found in this study (152° 15' 24.463" W). In part, 170° W is used because of its approximate alignment with the known ecological boundary at Samalga Pass (169° 28' 58" W). Samalga Pass demarks the last area in the AIs with a strong freshwater signal from the Alaskan Coastal Current (Ladd *et al*., 2005). Furthermore, at Samalga Pass the AI shelf narrows and the Alaskan Stream, the major boundary current of the western AIs, moves shoreward (Favorite, 1967).
* Benefits
  + Benefit of getting better estimates of life-history parameters if they really do vary with space (Thorsen *et al*., In Press). Provide justification for their variation ().
  + Don’t need data from every year
  + Stock definition methods based on life-history parameters often require synchronous sampling of the hypothesized stocks, a requirement that is not necessary here. For instance, Cope and Punt () had to restrict their analysis to only locations that were sampled every year, significantly limiting the breadth of their analysis.
  + Benefit of state-space models – observation and process: state-space models that although also seen as a step forward, with their ability to account for process and observation error, can lead to biased estimates of the strength of density dependence, particularly when indices of abundance appear oscillatory (Thorsen *et al*., In Press).
  + Models that partitioned space may have generated biased estimates of life-history parameters falsely leading scientists to believe that life-history parameters were or were not homogeneous between two different areas.
  + Obtain an estimate for the mean population growth while accounting for local variation
  + Using life-history characteristics to classify stocks has many important advantages. Data is often available either from idependent surveys conducted by the management agency or fishery data. Simple methods may only require a single year of data.
  + Genetic data sufficient to delineate between stock boundaries is often not available (Reiss *et al*., 2009).
  + Making the assumption that process noise is neglible and can be ignored, as done when using generalized linear models, one will underestimate true uncertainty in population trends. Confidence interval coverage in SSM improves with time-series length (Humbert et al., 2009), estimates of precision do not increase with only one or two decades of data, instead much longer time series are needed to augment precision (Flesch, 2014; Hinrichsen and Holmes, 2010; Ward *et al*., 2010).
* Downfalls of the method
  + Need lots of data
  + Species with inherently patchy distributions lead to an increased rate of non-convergence unless the mesh is extremely coarse.
  + Unequal vulnerability to gear between Japanese and US fleets limited our analysis from 1990 to present, furthermore data from the Bering Sea, although it was spatially adjacent and is managed by the same regional office (NPFMC), was not included because of different sampling mechanisms. If stocks can be found intermixing in space, sampling at a consistent time each year will limit the variation in dispersal leading to more robust results. The timing should relate to spawning times, which will in turn assist in representing population characteristics because of the limited dispersal and isolation of spawners which contribute to distinct populations although they may feed together.
  + Similarities does not imply population connectivity
  + Similarities may be indicative of matched responses to similar fishing pressure.
  + May not be the best method for mackerel because adult mackerel are less common than juvenilles, if not absent, from the standardized eastern BS bottom trawl survey (Lauth and Acuna, 2009).
* political often default, and biological stock boundaries is not new nor isolated. In fact the mismatch is often offered as an explanation on the lack of recovery for iconic stocks such as the North Sea cod ().

Conclusion: observed population structures invalidate current management policies. Indeed, one prerequisite for sustainable management is the matching of biological processes and management action (Reiss *et al*., 2009). The results from the present study clearly indicate that the population of cod in Alaska is not homogenous. Disregard of stock structure and ineffective fisheries management can lead to dramatic changes in the biological attributes and productivity rates, as well as the genetic diversity of the species. In view of this, and given the considerable commercial value of Alaskan cod fisheries, studies into the effects of oceanographic features on cod distribution and their population structure need to be continued. They also need to be taken into account in any future cod management strategy.

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# Tables

Todo: result tables

Table

# Figures

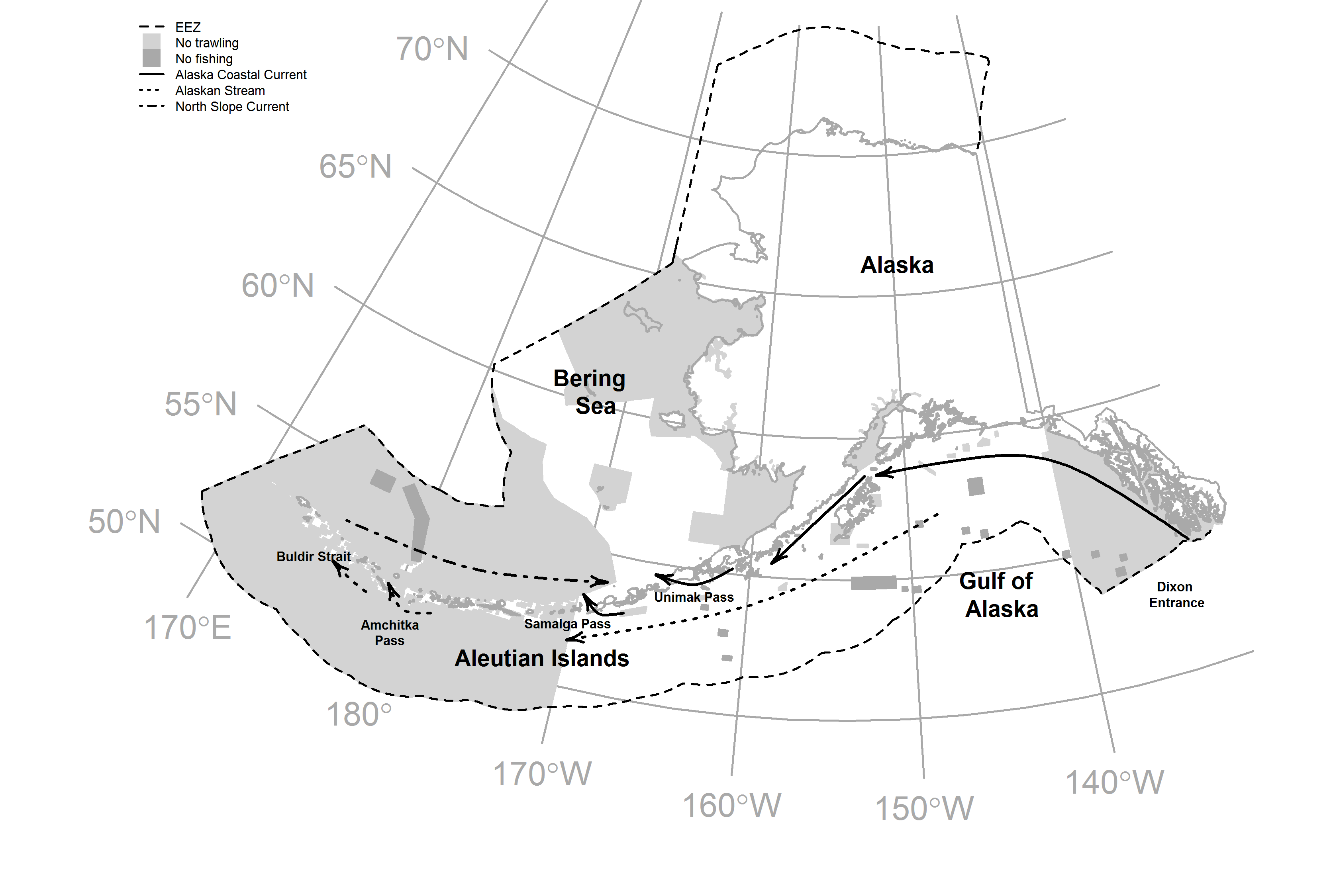


Figure 1. Map of the study area with major currents. Dashed line marks the United States Exclusive Economic Zone (EEZ). Dark gray polygons are areas with no fishing and light gray polygons are areas with no trawling. The light gray polygon near Dixon Entrance demarks the Southeast Alaska Outside Trawl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

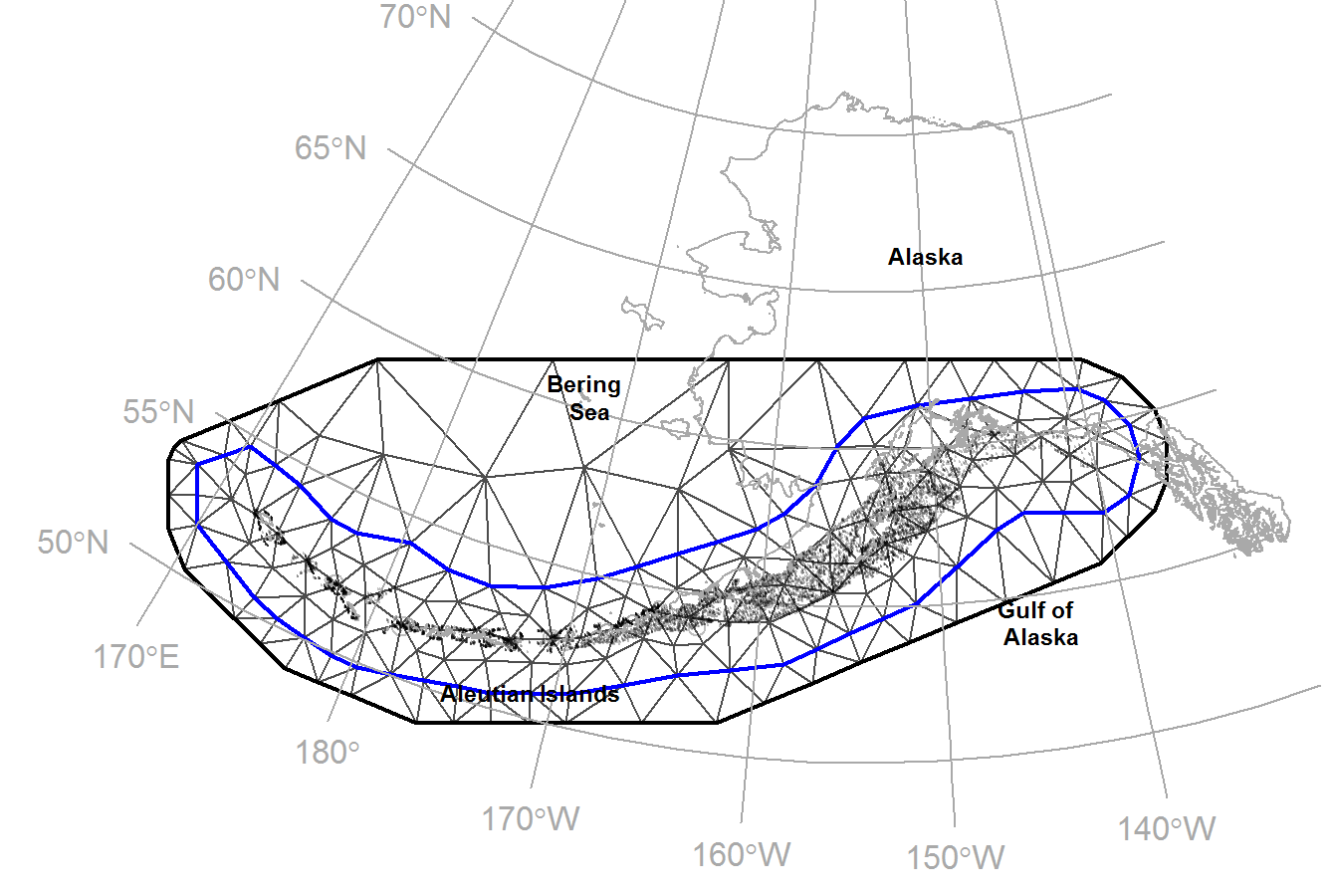


Figure 2. Catch per unit effort (CPUE, kg ha-1) for Pacific cod for all years (1990-2013). Point size is proportional to the maximum observed CPUE and points are shown with transparency to depict areas with higher sampling effort. Black lines display the triangulation mesh used to approximate a continuous 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.

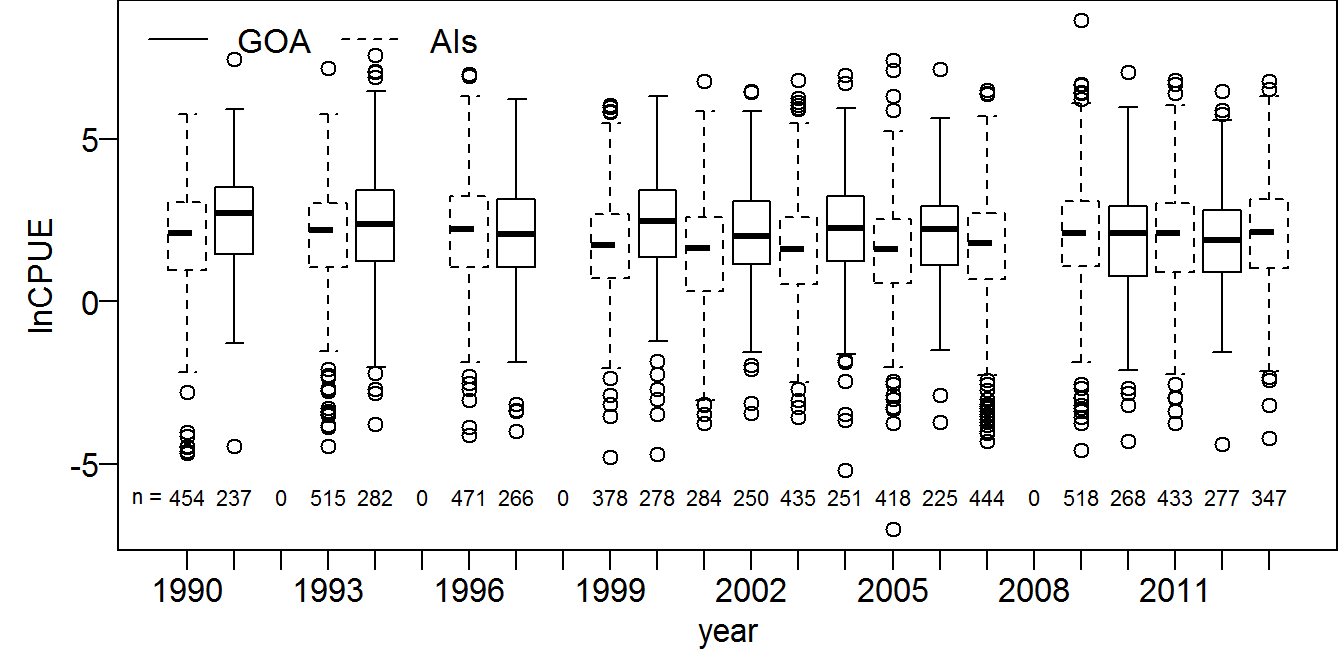


Figure 3. Yearly variation in non-zero catch per unit effort (CPUE, kg ha-1) measurements on the natural log scale for Pacific cod between stations sampled in the Gulf of Alaska (solid lines) and Aleutian Islands (dashed line).

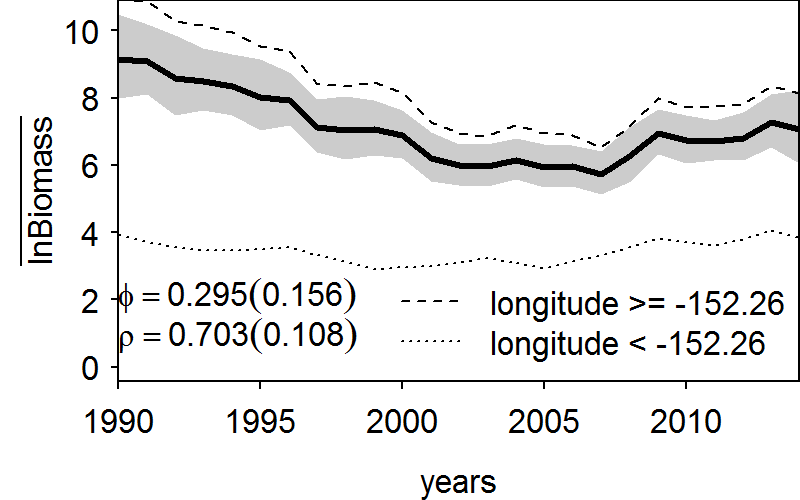


Figure 4. Estimated mean natural log biomass for the entire study area (i.e., Aleutian Islands and the Gulf of Alaska). Parameter estimates along with their standard errors, in parentheses, are given for i) density dependence (ρ) and ii) the log-ratio of expected abundance in the initial year (*t*=1)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

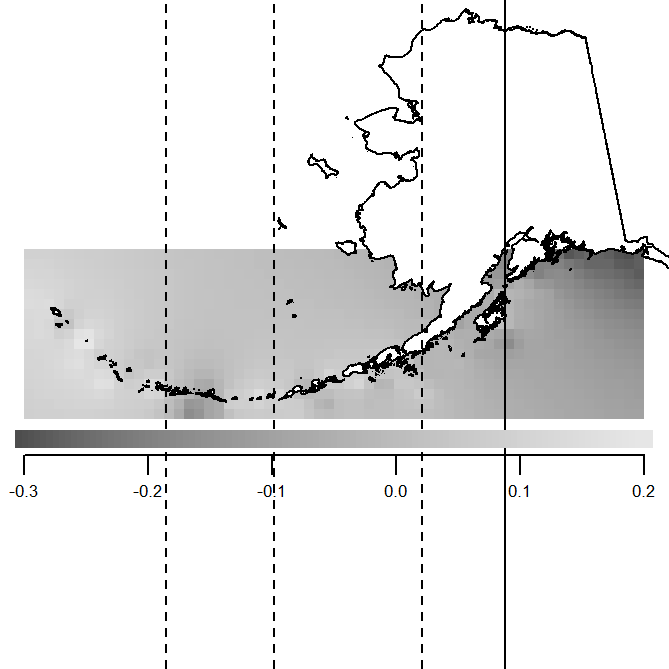


Figure 5. Spatial variation in productivity (EΩ) displayed using inverse distance weighting, where colors are proportional to the estimated value. Vertical solid line demarks hypothesized stock boundary and vertical dashed lines demark hypothesized stocks which were pruned from the final regression tree.

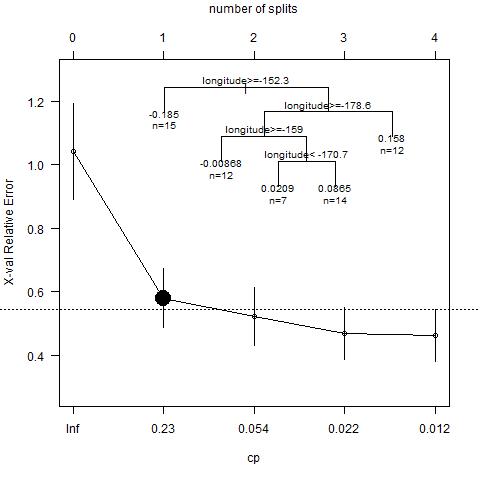


Figure 6. Cross validated relative error versus a complexity parameter (cp) to determine optimal pruning, where splits define distinct stock boundaries. The large black dot represents the best number of splits, with the location of each split displayed in the upper left inset. Regression trees worked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