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Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence

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Abstract

Identifying spatiotemporal hotspots is important for understanding basic ecological processes, but is particularly important for species at risk. A number of terrestrial and aquatic species are indirectly affected by anthropogenic impacts, simply because they tend to be associated with species that are targeted for removals. Using newly developed statistical models that allow for the inclusion of time-varying spatial effects, we examine how the co-occurrence of a targeted and non-targeted species can be modeled as a function of environmental covariates (temperature, depth) and interannual variability. The non-target species in our case study (eulachon) is listed under the US Endangered Species Act, and are encountered by fisheries off the US West Coast that target pink shrimp. Results from our spatiotemporal model indicate that eulachon bycatch risk decreases with depth and has a convex relationship with sea surface temperature. Additionally, we found that over the 2007-2012 period, there is support for an increase in eulachon density from both a fishery dataset (+ 40%) and a fishery independent dataset (+ 55%). Eulachon bycatch has increased in recent years, but the agreement between these two datasets implies that increases in bycatch is not due to an increase in incidental targeting of eulachon by fishing vessels, but because of an increasing population size of eulachon. Based on our results, the application of spatiotemporal models to species that are of conservation concern appears promising in identifying the spatial distribution of environmental and anthropogenic risks to the population.

Keywords: spatiotemporal, hotspots, endangered species, fisheries closures, marine protected areas, eulachon, shrimp, INLA

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Introduction

Interest in the spatial modeling of species' distributions has rapidly increased over the last 20 years (Guisan and Thuiller 2005, Phillips et al. 2006). Specific questions of interest range from modeling the occurrence or presence of a species over space (Elith et al. 2006, MacKenzie et al. 2006), to spatial variation in abundance (Austin 2002), and positive or negative correlations after explaining environmental drivers (Latimer et al. 2009, Ovaskainen et al. 2010). Understanding interactions between spatial and temporal variation of a species has implications for conservation and management, particularly as species face emerging threats, such as climate change (Walther et al. 2002). Assuming that the environment a population inhabits is heterogeneous in time or space and failing to consider the interaction (e.g. that the spatial distribution of good and bad habitat changes over time), is likely to lead to biased estimates of how that population will respond to disturbances. The statistical methods to disentangle spatiotemporal effects from environmental variables are complex, but recent computational advances have made these complex models more accessible to ecologists (Wikle 2003, Ward et al. 2012, Shelton et al. 2014).

A natural extension of the single-species case is asking how species associations change over time and space (Veech 2013). Species co-occurrence can be used to estimate interactions such as competition or predation (Ovaskainen et al. 2010), predict inhabited areas of cryptic species (Pearson et al. 2007, Thorson et al. 2014), identify attributes that may make species prone to range shifts as a result of changing climate (Amorim et al. 2014), and predict the effects of invasive species in new environments (Daehler 2003).

Species' co-occurrence data can also be used to evaluate human impacts on ecosystems, for example when human harvest results in simultaneous removal of target and non-target species. Anthropogenic activity may have predictable impacts on species that are targeted for

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removal, but less predictable impacts on non-target species that co-exist with target species. Impacts on non-target species often arise when non-target species co-occur with commercially valuable target species, such as in most fisheries (Pope et al. 2000, Branch et al. 2013), or in the hunting of game meat (Hofer et al. 1996). However, non-target species might also be affected when target species have little commercial value; for example, when the removal of nuisance species also negatively impacts non-nuisance species (Gribble et al. 1998, Eason et al. 2002). The unintended effects on non-target species may be of greatest concern when the non-target species is of conservation concern (Roe et al. 2014). For both target and non-target species, it is particularly important to understand the effects of environmental variables on distribution and abundance, as these factors may interact with anthropogenic impacts. Examples may include interactions between the spatiotemporal distribution of temperature (which may affect a species' range) and the distributions of human disturbance (harvest, pollutants).

To illustrate the spatiotemporal modeling of a target and non-target species, we focus on interactions between eulachon (Thaleichthys pacificus), a threatened species, and pink shrimp (Pandalus jordani) from the Northeast Pacific Ocean. Eulachon (also known as 'Pacific smelt' or 'candlefish') are a small, anadromous forage fish, historically commercially valuable, and culturally important (Senkowsky 2007, Reynolds and Romano 2013). Eulachon serve as a source of prey for higher trophic level species because individuals contain high lipid content and form large spawning aggregations (Sigler et al. 2004). Spawning runs of eulachon in Canada and the USA began to decline from highs in the mid-20th century (Hay and Carter 2000, Gustafson et al. 2010), and were listed as threatened under the US Endangered Species Act (ESA) in 2010. The two main obstacles to recovery are (1) long term effects of climate on ocean conditions, and (2)

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bycatch, as non-target species in commercial fisheries (National Marine Fisheries Service West Coast Region 2013).

Here we show how spatiotemporal models can be used to assess the co-occurrence of a target (pink shrimp) and a non-target species (eulachon) to achieve three management goals relevant to the threatened species. First, to estimate and validate the population trend of eulachon over the past decade, we apply spatiotemporal models to two spatially explicit data sets - one fishery-independent and one fishery-dependent. Next, to understand the bycatch risk faced by eulachon as a non-target species, we combine the spatial estimates of eulachon density with spatial estimates of pink shrimp density and create time-varying maps of bycatch risk along the coast. Pink shrimp are commercially important on the US west coast, but the shrimp fishery is also the main source of eulachon bycatch along the US west coast. Finally, to provide information that could reduce future bycatch rates, we compare the bycatch risk across years to ask if there are persistent bycatch hotspots across the time series, and whether environmental covariates may be used to predict areas of high bycatch risk. Similar spatial models have been applied to fisheries data (Viana et al. 2013, Pennino et al. 2014, Cosandey-Godin et al. 2015), but these methods have not been extended to deal with multiple species, or applied to threatened and endangered species. Combining different spatially explicit datasets, our analyses provide fisheries managers information on both annual trends of a protected species, as well as specific spatial areas that may be targeted for future management actions.

Methods

Data

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We used two spatial data sets from the west coast of the United States: fishery-dependent shrimp and eulachon catch data (kg) from the West Coast Groundfish Observer Program (WCGOP) at the Northwest Fisheries Science Center (NWFSC) (Al-Humaidhi et al. 2012) and fishery-independent survey data of eulachon from the west coast trawl survey, collected by NWFSC between 2003 and 2012 (Bradburn et al. 2011). While eulachon are captured by several fisheries in the Northeast Pacific, we focused our analysis on the pink shrimp trawl fishery off the northern California, Oregon and Washington coasts, because it is associated with > 99% of the observed eulachon caught as bycatch (Bellman et al. 2011; Fig. 1; Table 1). The pink shrimp season spans April-October, and during this period WCGOP observes as much as 20% of pink shrimp trawls (Bellman et al. 2011). Whether differences exist in the spatial or temporal distribution of observed and unobserved vessels is unknown, but the observed vessels are assumed to be representative of all vessels. We restricted our analysis spatially to the coastal area where eulachon have been observed (> 41ºN), and temporally to sequential years with observer coverage, 2007-2012 (the fishery did not include observers in 2006).

The average latitude and longitude of each shrimp trawl were used to represent the spatial locations of each sample, and these values were converted to UTM zone 10. In addition to the spatial locations, we considered two spatially referenced covariates, depth (ftm) and sea surface temperature (SST) that may help explain the distribution of shrimp and eulachon densities. Both variables are thought to influence catchability, with depth as a proxy for light, and SST a function of upwelling (Pearcy 1970, Hannah 2011). The average depth of each trawl (ftm) was treated as a linear and quadratic predictor, following similar estimated relationships between depth and groundfish (Shelton et al 2014). As an environmental covariate, we used fine scale SST anomalies using both linear and quadratic predictors. For each trawl, we collected daily SST

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anomalies on a 0.25º grid, and used bilinear interpolation to create SST values corresponding to each location in the dataset (http://www.esrl.noaa.gov/psd/, Reynolds et al. 2007). Like other species distribution models, this framework is easily extended to include other static or time-varying habitat characteristics as predictors.

Trends in eulachon density inferred from fisheries data alone may be biased for several reasons: fishing is not random in space or time, but is done preferentially, (2) vessels with observers on board may behave differently than those without, and (3) the resolution of species identification may vary slightly from observer to observer (from 2007-2009 before eulachon were listed under ESA, some observers separated them from other smelt species, while other observers may not have). We attempted to validate our estimated trends in eulachon density by fitting similar spatiotemporal models to data from a fisheries independent trawl survey data collected by NWFSC between 2003 – 2012. This dataset has used the same methodology over the time series (stratified random sampling design, with the same bottom trawl sampling gear throughout the time series), and provides an external index of changes in eulachon density (Bradburn et al. 2011). Over the period 2003-2012, eulachon were encountered in 9% of 3455 research vessel hauls. For spatial consistency between datasets, we only include trawls conducted north of 41ºN.

Statistical modeling

We constructed separate models for shrimp and eulachon data to understand the spatiotemporal patterns of eulachon and shrimp density, as well as how their interactions may lead to increased eulachon bycatch risk. We adopted this approach of modeling them independently instead of modeling the ratio of eulachon / shrimp density directly, because it

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allows for the effect of covariates on species distribution to differ between species and allows separate estimates of shrimp and eulachon temporal trends. For eulachon, either bycatch numbers or weight could be used as the response variable; we used weight (kg) because it captures overlap in terms of both numbers and individual size, and thus better represents the spawning potential for the eulachon population. Because eulachon were absent from a large number of observed shrimp hauls (38% of 8723), we separately modeled the presence and distribution of eulachon density, adopting a delta-GLM approach with two sub-models (Pennington 1983, Maunder and Punt 2004, Thorson and Ward 2013). Probability of occurrence of eulachon in year *t* for a set of locations **s** was modeled using a binomial GLMM with logit link,

$$\text{logit}\big(\boldsymbol{p}_t(\mathbf{s})\big) = \mathrm{X}_t(\mathbf{s})\boldsymbol{b} + \varepsilon_t(\mathbf{s}) \quad (1)$$

where $\boldsymbol{p}_t(\mathbf{s})$ represents the probabilities of eulachon occurrence at locations **s** in year *t*, $\mathrm{X}_t(\mathbf{s})$ represents a matrix of fixed effect covariates at locations **s** in year *t* (Depth, Depth^2, SST, SST^2, Year), $\boldsymbol{b}$ represents a vector of coefficients to be estimated, and $\varepsilon_t(\mathbf{s})$ represents a vector of spatial random effects that follow a first-order autoregressive process:

$$\varepsilon_t(\mathbf{s}) \sim Normal\big(\rho \cdot \varepsilon_{t-1}(\mathbf{s}),\ \Sigma\big) \quad (2)$$

where ρ represents the degree of autoregression in encounter probabilities and Σ represents spatial covariation in random effects (discussed below). Further details regarding the covariance among locations and years can be found in Thorson et al. (In press). Spatial random effects were assumed to be autoregressive to account for variation not explicitly included in our model (variation due to the environment or population processes such as density dependence). To model the distribution of eulachon density as the second sub-model, we assumed that the log of eulachon density was normally distributed, and modeled as

$$\log\left(\boldsymbol{u}_t(\mathbf{s})\right) = \mathrm{Z}_t(\mathbf{s})\boldsymbol{c} + \delta_t(\mathbf{s}) + \log\left(E_t(\mathbf{s})\right) \quad (3)$$

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$$Y_t(\mathbf{s}) \sim \text{Lognormal}(\boldsymbol{u}_t(\mathbf{s}), \sigma) \quad (4)$$

where $Z_t(\mathbf{s})$ is a matrix of covariates corresponding to each haul location (similar to $X_t(\mathbf{s})$), $\boldsymbol{c}$ represents the estimated coefficients, $\delta_t(\mathbf{s})$ represent spatial random effects that again follow an autoregressive process (similar to eqn 2, but with a unique covariance matrix), $E_t(\mathbf{s})$ represents the duration of hauls as a measure of effort, included as an offset (Thorson and Ward 2013), and σ represents a residual error term for the lognormal distribution.

For both covariance matrices of the spatial random effects in the presence-absence and positive models, we used the Matern function to model covariance as a function of Euclidian distance, $\Sigma_{i,j} = \frac{\tau^2}{\Gamma(\nu)2^{\nu-1}}\left(\kappa \cdot d_{i,j}\right)^{\nu} K_{\nu}\left(\kappa \cdot d_{i,j}\right)$, where $\Sigma_{i,j}$ is the modeled covariance between locations *i* and *j*, τ^2 is the estimated spatial variance, $\Gamma()$ and $K_{\nu}()$ represent the gamma and Bessel functions, respectively, $d_{i,j}$ is the Euclidian distance between locations *i* and *j*, and κ is an estimated scaling parameter (Lindgren et al. 2011). The parameter ν controls the smoothness of the Matern function and is usually fixed rather than estimated from data (when $\nu = 0.5$, the Matern reduces to the simpler exponential covariance function). Following previous work, we chose $\nu = 3/2$; this allows the Matern to be more flexible than the exponential, but also allows the function to be differentiable (Rasmussen & Williams 2006). The covariance matrices for the presence-absence and positive models each have separate parameters τ^2 and κ, reflecting the assumptions that each model component may have a different variance or rate at which correlations decline as a function of distance. Further details can be found in (Ono et al. 2014, Thorson et al. 2014).

We applied the same delta-GLM model formulation (eqn. 1-4) to eulachon and pink shrimp in both the fishery observer data (2007-2012) and to eulachon in the fishery independent trawl survey (2003-2012). Though our analysis was primarily interested in the dynamics of

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eulachon, fitting these spatiotemporal models to data from the target species (shrimp) allows us to generate spatial predictions of the distribution of bycatch. Pink shrimp are encountered in the majority of the shrimp fishery hauls (> 95%, Table 2), but there is wide variation in total density caught. Like eulachon, we included depth and temperature as quadratic predictors of shrimp density, year as a fixed effect, and autoregressive spatial random effects. In all, we fit a total of 3 spatiotemporal models, each with a presence-absence and positive-catch component (Table 2): one delta-GLMM model for eulachon and one delta-GLMM model for shrimp in the fishery dataset (spanning 2007-2012); and one delta-GLMM model for eulachon in the fishery independent dataset (spanning 2003-2012).

Estimation of latent Gaussian Markov random fields has been difficult, and can be challenging in a Bayesian framework if the dimensionality of the knots or locations is large (Shelton et al. 2014). Recent advances have allowed the spatial covariance matrix to be approximated via stochastic partial differential equations (SPDE) as calculated within INLA (Rue et al. 2009, Ruiz-Cardenas et al. 2012). More specifically, INLA approximates the inverse of the spatial variance-covariance matrix of fixed locations using three large sparse matrices (see Thorson et al. In press for more details). Estimation of the fixed effects is then done via maximum marginal likelihood using the Laplace approximation to approximate the integral across random effects, and random effects are estimated via Empirical Bayes. Using these estimates (and Bayesian priors on fixed effects), INLA allows Monte Carlo samples to be generated from the posterior distribution, as the Laplace approximation to the marginal likelihood. Another advantage of the SPDE-INLA approach is that estimation is done entirely in a predictive modeling framework. Instead of validating model predictions with a test and training subset, the predictive density of each data point can be found, based on predictions from latent

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228 random effects. We calculated two models of predictive accuracy: for the presence-absence
229 model, we calculated the area under the curve (AUC) estimate from the receiving operator
230 characteristic curve (ROC) using the ROCR package in R (Sing et al. 2005), and for the positive
231 model, we calculate the proportion of observed values that fell within the 95% credible intervals
232 of the predictions.
233 *Interpreting results from statistical modelling*
234 After fitting the three delta-GLMM models (to fishery-dependent information regarding
235 catch rates of shrimp and eulachon, and to fishery-independent data for eulachon, see Table 2),
236 we then interpret our results in three main ways. First, to display spatial variation in density for
237 each species, we generate maps of abundance for shrimp and eulachon. Second, we used
238 estimated indices of coastwide abundance to assess whether different data sources are in
239 agreement regarding trends in catch rate for each data set. Third, to identify regions of relatively
240 high or low bycatch risk, we compared fishery-independent estimates of eulachon density with
241 fishery-dependent estimates of eulachon catches, and generate maps representing bycatch risk for
242 eulachon. Each of these analyses is explained in detail below.
243
244 *Analysis #1: Assessing spatiotemporal trends in abundance*
245 After estimating the models above, we divided our study area (Fig. 1) into 1-km grids.
246 We used the SST value along with average fishing depth (77 ftm) to project the estimated
247 eulachon density onto the center of each grid cell. The estimated predicted values at each of the
248 grid cell centers was calculated given the estimated fixed effects and random effects at the mesh
249 locations (Latimer et al. 2009; Lindgren et al. 2011), and these values for each of the delta-GLM
250 sub models was then transformed back to normal space using the appropriate transformation

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(logit^{-1}, log^{-1}). Total density was calculated by multiplying estimated occurrence at each grid location by the estimated density from the positive model at that location (Shelton et al. 2014). Total eulachon density for each year was calculated by summing estimates across 1-km grid cells (the mean and CV across grid cells were also calculated as summary statistics). To include uncertainty in these estimates, we generated 5000 samples from the approximated posterior distribution, using the inla.posterior.sample() function. The projection and total density calculation was repeated for each of these 5000 posterior samples, yielding standard deviations and credible intervals of density estimates. This procedure was repeated for both the eulachon and pink shrimp delta-GLM sub-models to create annual indices of both species.

Analysis #2: Estimating indices of abundance from each data set

We compared the total eulachon density from the pink shrimp fishery dataset to the total eulachon density from the fishery independent bottom trawl dataset to examine the concordance in the annual trends in eulachon density. Because the shrimp fishery and NWFSC trawl survey datasets have different eulachon catch rates, we standardized them to a similar relative scale, dividing each density estimate by the estimated density in 2007 (the first year of data from the pink shrimp fishery). This standardization procedure was replicated for each Monte Carlo sample from the approximated posterior distribution, so that the estimate in 2007 was always 1.0. To summarize the average annual trends of our estimates, we fit univariate state-space time series models to each, using the MARSS package in R (Holmes et al. 2012).

Analysis #3: Identifying bycatch hotspots and spatial patterns of abundance

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Following the projection methodology described above, we used the models fit to the pink shrimp fishery dataset to generate spatial predictions of both eulachon and shrimp density, as well as the bycatch ratio for each year, 2007-2012. The bycatch ratio at each location was calculated as the ratio of eulachon to shrimp density; thus, the estimated bycatch ratio at each location is derived from the estimates of the fishery-dependent eulachon delta-GLMM model and fishery-dependent shrimp delta-GLMM model. We calculated uncertainty bounds by taking Monte Carlo samples from the approximated marginal likelihood from each model projection and calculating the bycatch ratio. Mapping the distribution of bycatch ratios provides a visualization of bycatch risk in each year. To determine if areas associated with high bycatch risk were persistent across years, we identified the 1-km grid cells with the largest 10% of the bycatch ratio in each year and counted the average number of years each grid cell fell in the top 10% of bycatch risk.

Finally, we examined how spatial variability changed through time and how this variation related to density estimates. The relationship between population size and spatial variability or patchiness has been widely studied in ecology (Brown 1984, Kareiva 1990, Hanski 1998). For example, pink shrimp have a strong correlation between population size and area inhabited (Hannah 1995). For marine fish species, increasing patchiness at low density may also affect recruitment or species rebuilding times (MacCall 1990). For species of conservation concern, like eulachon, a relationship between average density and the spatial variability of density would suggest whether density patchiness changes with overall abundance. Increased patchiness at low density would suggest a greater potential for fishing mortality to severely deplete local eulachon populations, suggesting that eulachon populations face increased risk of extinction at low density. Using eulachon density from the fishery-dependent pink shrimp delta-GLMM, we

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296 calculated the density for each 1x1km grid cell and coefficient of variation (CV) among grid
297 cells, for each year between 2007-2012, to look for changes in spatial patchiness with overall
298 density.
299
300 **Results**
301 *Analysis #1: Assessing spatiotemporal trends in abundance*
302 Spatiotemporal models of eulachon and pink shrimp revealed spatial and temporal
303 variability in density for both species, as well as bycatch risk. Between 2007 and 2012, average
304 effort in the pink shrimp fishery showed strong spatial patterning (Fig. 1). Shrimp and eulachon
305 density also showed strong variation in spatial distribution patterns but visual inspection shows
306 that areas of high density do not coincide between the species (Fig. 1). We found that both
307 shrimp and eulachon density were affected by environmental variables. Consistent with previous
308 modeling (Hannah 2014), eulachon occurrence and density decreased monotonically with depth.
309 The effect of depth was strongest for the occupancy model, which is expected given that
310 eulachon is a nearshore species (Fig. 2). The effect of depth on shrimp density was weaker, but
311 the quadratic effect indicated highest density at intermediate depths (~ 95 m, Fig. 2). The effect
312 of sea surface temperature was strongest for eulachon, with lowest occurrence and density
313 occurring at intermediate SST anomalies (~ -1, Fig. 2). Warmer SST anomalies corresponded to
314 slightly higher shrimp occurrence, and total shrimp density was also found to have a convex
315 relationship with SST (Fig. 2). From the estimated covariate effects predicting shrimp and
316 eulachon density, we can also examine how these variables affect derived bycatch risk.
317 Specifically, bycatch decreased with haul depth (Fig. 2). The effect of SST was convex on both

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the presence-absence and positive eulachon models (Fig. 2), suggesting lowest bycatch rates at temperatures near average ($u_{SST} = -1$), but higher bycatch rates at lower and higher anomalies.

Analysis #2: Estimating indices of abundance from each data set

Despite the strong spatial patterning, the average maps of eulachon density obscured a more general trend in abundance across years. Overall density estimates from the shrimp fishery and the independent trawl survey showed an increasing temporal trend in eulachon (Fig. 3). The exponential growth rate of estimated eulachon density since 2007 has increased by 39.7% (95% CIs = 26.1-54.5%) annually based on the shrimp fishery data and by 56.1% annually (95% CIs = 22.8-85.9%) based on the trawl survey. Despite the different methodology and gear used in each dataset, the 10 year window provided by the fishery-independent research survey suggests that the eulachon density was substantially higher in 2012 than in any recent period (Fig. 3). We lack data to compare current density estimates to eulachon density in historical times.

Analysis #3: Identifying bycatch hotspots and spatial patterns of abundance

Output from the eulachon and shrimp models applied to the shrimp fishery data were combined to generate year specific maps of eulachon bycatch risk (Fig. 4). These maps suggest bycatch risk increasing in recent years. Examining projected bycatch rates over time, our spatiotemporal model suggests several areas that have higher or lower bycatch rates, on average, after accounting for environmental covariates and year-to-year variation (Figs. 2-3). Examining areas associated with the top 10% risk in each year indicates that these high risk areas are primarily in coastal areas and generally consistent across time: three examples include the area just south of Coos Bay (Oregon: CB in Fig. 5), the area south of Greys Harbor (Washington: GH

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in Fig. 5) north of the Columbia River, and the area just south of La Push (not shown) in the middle of the Washington coast (Fig. 5). Areas further offshore appear to have lower estimated bycatch rates, which is not surprising given that eulachon are a coastal pelagic species. While some hotspots appear to be consistent over time, there is also considerable variation across years; bycatch risk in 2012 is notably different from previous years, for example. We do not have an explanation for the radically different patterns of bycatch risk in 2012 but note it occurred in a year of unusually high eulachon abundance (Fig. 3).

Finally, we summarized the relationship between the spatial variation and mean density of eulachon across the study area. Overall, there is a notable negative relationship between total eulachon abundance and the spatial variability in eulachon density (Fig. 6). This indicates that eulachon density has become less patchy over the course of the time-series. Together, these results suggest a potential for density-dependent distribution of eulachon density that should strongly inform potential management actions for this threatened species.

Discussion

The importance of spatiotemporal variability in population processes has long been recognized in ecology. Until recently, fitting these models to data has been computationally prohibitive because of their complexity, with hundreds or thousands of spatial random effects being potentially estimated. Instead, ecologists have tended to focus on the singular effects of space or time, while ignoring potential interactions. Understanding how the distribution of a population (and the spatial variation) changes over time is critical for commercially valuable species targeted for harvest and species of conservation concern (Viana et al. 2013, Thorson et al. 2014). We show how spatiotemporal models can be used to develop approximate Bayesian

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364 estimates and inform multiple management aspects of two interacting marine species (targeted
365 pink-shrimp and non-targeted eulachon).

366 In the Northeast Pacific Ocean, eulachon are known to co-occur with a range of other fish
367 species, such as pollock and herring, as well as invertebrates, such as krill (Wilson 2009).
368 Understanding the interactions in space and time with pink shrimp is particularly important for
369 fisheries management, where the goal is to minimize eulachon bycatch while achieving pink
370 shrimp landings near maximum sustainable yield. Spatiotemporal models, such as those used in
371 our analysis, may be useful in identifying separation in the spatial, temporal, or depth
372 distributions of these species. We found strong support for differences in the occurrence of these
373 species at different depths, which is somewhat expected given their life histories (eulachon tend
374 to be more pelagic feeding on plankton near the surface, and adult shrimp tend to occupy sandy
375 or muddy ocean bottoms). Similarly, our models also found support for consistent hotspots of
376 eulachon in areas off the Oregon and Washington coast, which may represent pre-spawning
377 aggregations

378 In our examination of the spatiotemporal distribution of eulachon incidentally caught by
379 the pink shrimp fishery off the US west coast, we demonstrated three advantages of this
380 modeling approach. First, these methods may be used to assess overall trends in abundance,
381 similar to simpler population viability (PVA) style approaches. Estimates derived from the
382 spatiotemporal model are more robust than estimates that ignore spatial variation (Dormann
383 2007; Thorson et al. 2014). For eulachon, the positive trends in estimated density over 2007-
384 2012 (Fig. 3) provides an optimistic outlook for eulachon recovery. Because this trend was found
385 in the dataset from the fishery and the independent research dataset, it is more likely that
386 increasing eulachon bycatch is attributable to an increasing eulachon population, rather than

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increasing bycatch rates. The differences between the two trend estimates may be partially explained by shrimp fishing vessels becoming more efficient at avoiding eulachon over this period (Hannah and Jones 2007, 2012), which would cause the trend in eulachon density estimated from fishery data to be underestimated. Though not included in our analysis, increases of similar magnitude to those found in our study have also been found in marine surveys in Canadian waters encountering more northern populations of eulachon (Schweigert et al. 2012). Another hypothesis for increased eulachon bycatch is that shrimp density has declined, however this decline is not supported by the data (Fig. 3).

A second result of the spatiotemporal modeling approach is that by combining species abundance with covariates that are also changing in space and time, the effect of these covariates on occurrence or abundance can be estimated, and maps of species distributions can be generated. For eulachon, we found that the depths of each shrimp haul were negatively correlated with occurrence and total density (Fig. 2). We also found a convex relationship of ocean temperature on eulachon occurrence and density, suggesting that larger eulachon density may be found at extreme temperatures (Fig. 2). Variables like ocean temperature, which vary at wide spatial scales, can be useful in producing spatial maps of abundance or bycatch risk (Fig. 4). Though our projections are temporally coarse on an annual time step, similar projections could be made on weekly, or even daily time steps. For some marine species, fisheries managers have instituted mobile closures in time and space (Grantham et al. 2008, Haflinger and Gruver 2009), and fine scale spatiotemporal projections may be useful in informing in-season fisheries closures.

The third output from our case study is that we can ask whether areas associated with high bycatch risk are consistent over time. For eulachon encountered in the shrimp fishery, we found at least three areas that appear to be consistent hotspots of eulachon bycatch across years

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(Fig. 5). For some relatively sessile species, such as rockfish species, managers have designated protected areas that are static across time (Dalton and Ralston 2003). Though the mechanism for higher eulachon bycatch rates in these areas across years is unclear, our general approach may be useful in identifying candidate areas for future fishery restrictions or closures.

A number of approaches have been successfully implemented to minimize impacts on protected marine species, such as eulachon. In addition to fishing closures, other successful approaches include modification to fishing gear (Hannah et al. 2011). Spatiotemporal statistical models, similar to the approach used in this paper, are yet another tool for management that can also be used to identify ways to minimize risk, both temporally and spatially (see also: Jannot & Holland 2013). Because of recent advances in software tools, such as INLA, there are few computational hurdles involved in fitting these complex spatiotemporal models, and the only limit to application of these methods is the availability of spatially referenced data. Many trawl survey datasets in the USA, such as the one included in our analysis, have been made publicly available only recently, but we expect similar data to become available from other ecosystems around the world.

Acknowledgements

NOAA High Resolution SST data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/. Observer data provided by the Fisheries Observation Science program, and the fisheries independent trawl survey data provided by the Population Ecology program (NWFSC, NOAA). Additional assistance with interpretation was provided by staff from both programs. J. Thorson thanks K. Kristensen, H. Skaug, and S. Munch for ongoing input regarding interpretation of Gaussian random field

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433 modelling. B. Hannah (ODFW), R. Gustafson, M. McClure, and three anonymous reviewers
434 provided additional feedback that improved the quality of this manuscript.

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Description of Ecological Archives material

Included for the supplement are

1. A dataset for eulachon from the NOAA trawl survey, 2003-2012. Data are spatially referenced, and labeled with corresponding date. Response is the biomass encountered.
2. R code for fitting a spatiotemporal model to the eulachon trawl survey (fishery independent dataset)

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619 Table 1. Summary of observed effort, shrimp catches, and eulachon bycatch, 2007-2012 in
620 trawls targeting pink shrimp.

Summary	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Eulachon wt (kg)	199.204	348.23	364.95	1585.10	2965.47	4349.36
Eulachon occurrence (%)	0.07	0.24	0.28	0.65	0.70	0.90
Shrimp wt (kg)	1302.87	1249.73	1133.21	1851.44	4050.77	3655.25
Effort (haul hrs)	1649	1424.05	949.74	2091.29	3858.79	4249.3

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623 Table 2. Summary of datasets and model diagnostics used in our analysis. Included are the
624 species, data source ('Survey' = fisheries independent), time span, sample size (n = no. of hauls),
625 and for each a diagnostic measure of fit. For the presence-absence sub-model, we include the
626 area under the curve (AUC) from the receiver characteristic operating curve (ROC), where
627 values closer to 1.0 indicates better predictive abilities. For the positive model, we include the
628 proportion of observed data that fall within the 95% predicted credible intervals from the
629 spatiotemporal model.

Model	Species	Data source	Years	n	Response	AUC	95% coverage
1	Eulachon	Fisheries	2007-2012	9107	Presence	0.662	
	Eulachon	Fisheries	2007-2012	5524	Positive		0.982
2	Pink shrimp	Fisheries	2007-2012	9107	Presence	0.514	
	Pink shrimp	Fisheries	2007-2012	8723	Positive		0.979
3	Eulachon	Survey	2003-2012	3181	Presence	0.894	
	Eulachon	Survey	2003-2012	294	Positive		0.976

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631 **Figure Legend**

632 Figure 1. Spatial distribution of observed effort (measured as total haul duration in hours),
633 shrimp catch per unit effort (kg / haul hours), and eulachon bycatch per unit effort (kg / haul
634 hours), aggregated over 2007-2012. For scaling purposes, effort and catch per unit effort are
635 shown in log space.
636
637 Figure 2. Marginal posterior effects for the relationships between depth and sea surface
638 temperature (SST). Effects are shown separately for the presence/absence of eulachon, total
639 eulachon and shrimp density, and as the derived bycatch risk of eulachon:shrimp density. To
640 show the marginal effects, all covariates not of interest are held at the mean (77 ftm depth, SST
641 anomaly = -1). The relationship is shown across the entire observed scale, and the rug plot (i.e.,
642 ticks at the bottom of each plot) indicates the distribution of data.
643
644 Figure 3. Estimated density indices of eulachon from the Northwest Fisheries Science Center
645 trawl survey, 2003-2012, and from the pink shrimp fishery observer data, 2007-2012. Indices are
646 scaled to 2007 values (estimated posterior medians are presented, with +/- 1 sd). Also shown are
647 estimates of shrimp density +/- 1 sd (scaled by a factor of 10 to make estimates visible).
648
649 Figure 4. Estimated bycatch risk, projected from the posterior predictive distribution on a 1km
650 grid. Bycatch risk is calculated as estimated eulachon density / shrimp density. Orange / red
651 areas represent relative hot spots of eulachon bycatch; blue areas represent areas of low risk. All
652 years are shown on the same scale to show the increasing trend in eulachon/shrimp density.
653

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Figure 5. Estimated areas of highest bycatch risk, projected from the posterior predictive distribution on a 1km grid. For any year, bycatch risk is defined as the top 10% of values (shown in red); to show consistent areas across time, averages are calculated over all years. North to south: GH= Grey's Harbor, WA, NP=Newport, OR, CB= Coos Bay, OR, EU=Eureka, CA.

Figure 6. Estimated mean eulachon density (kg/km^2) and CV, 2007-2012. The 95% CIs are shown around the estimates of each summary statistic as solid lines.

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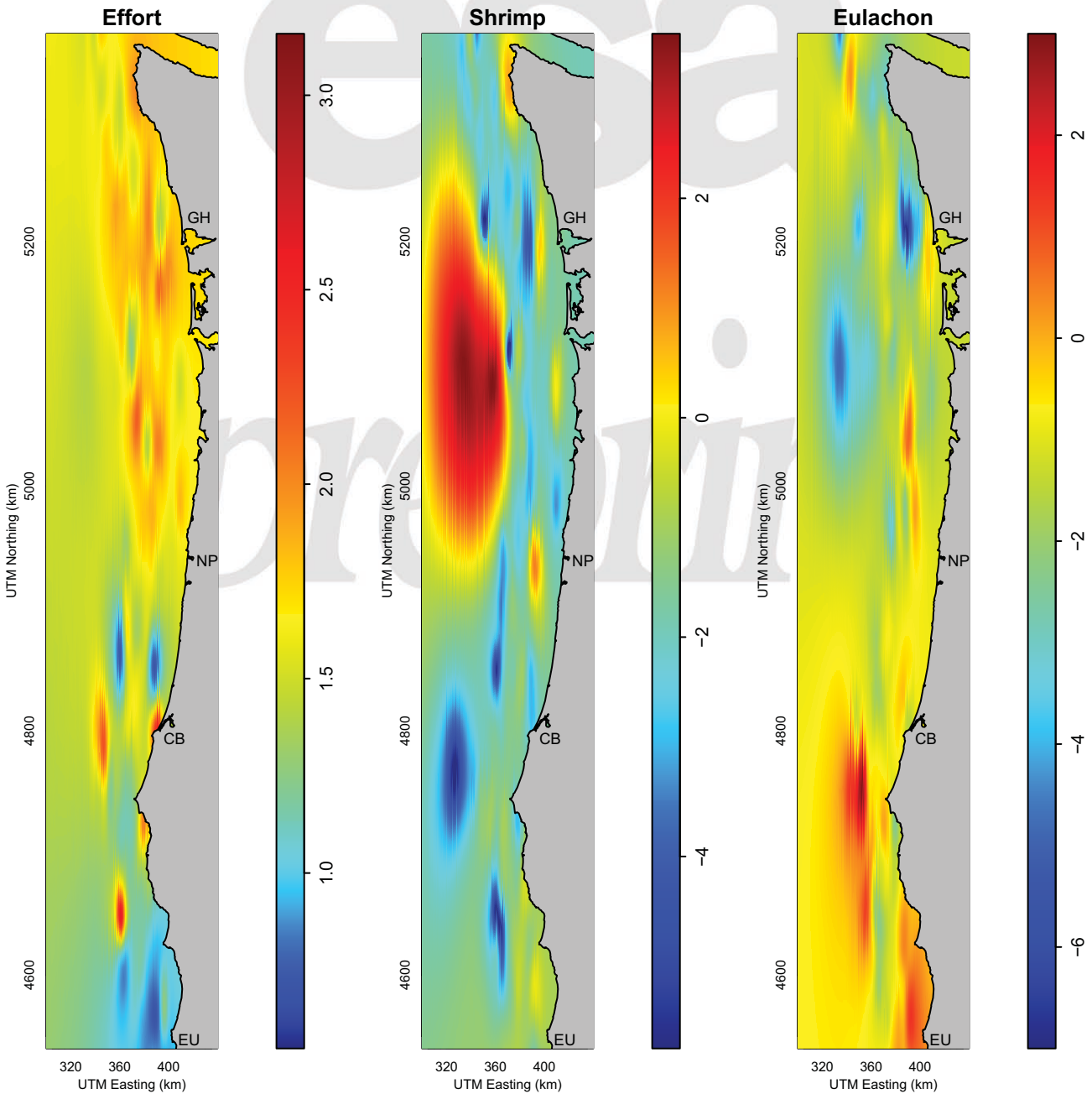

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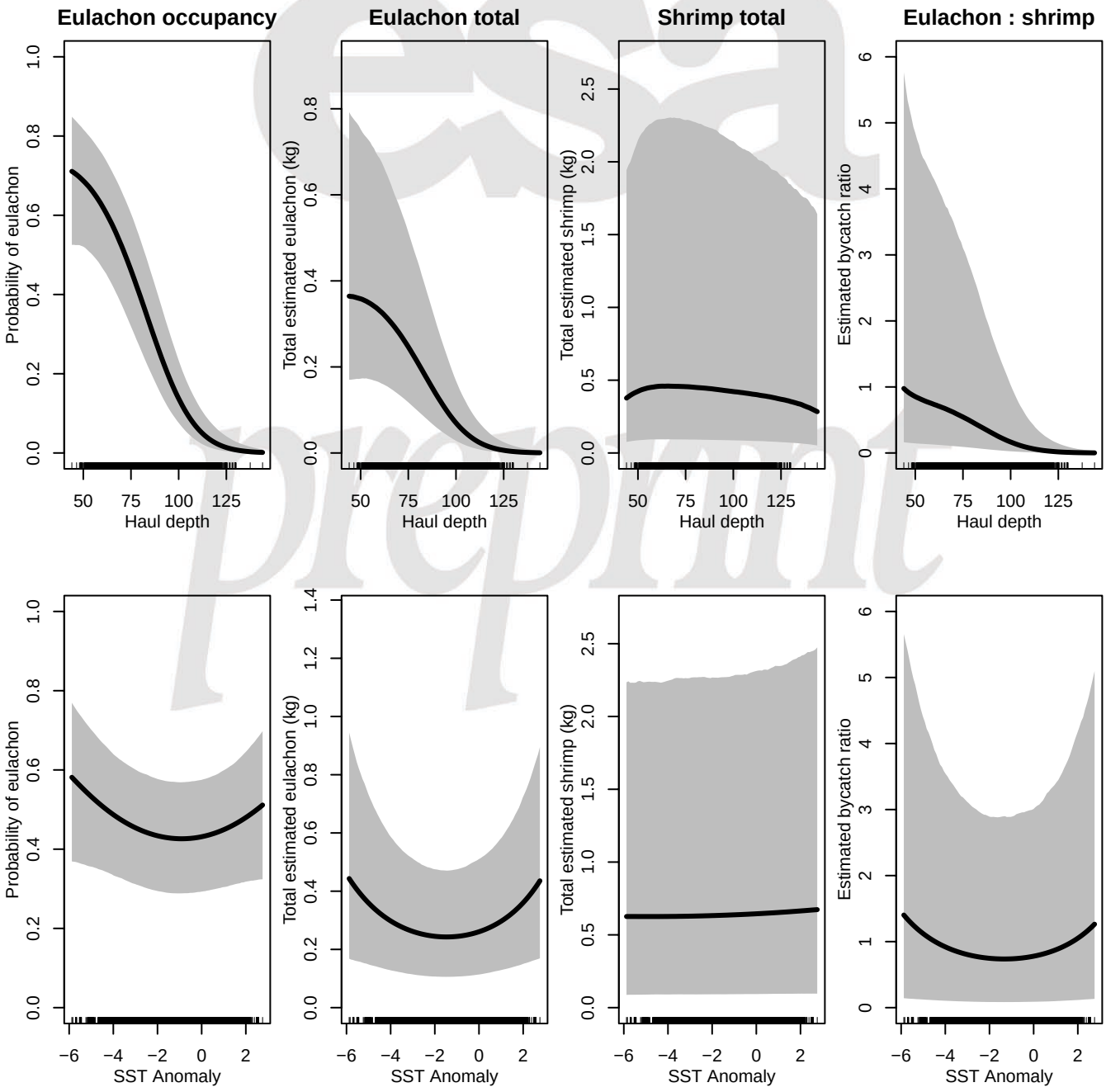

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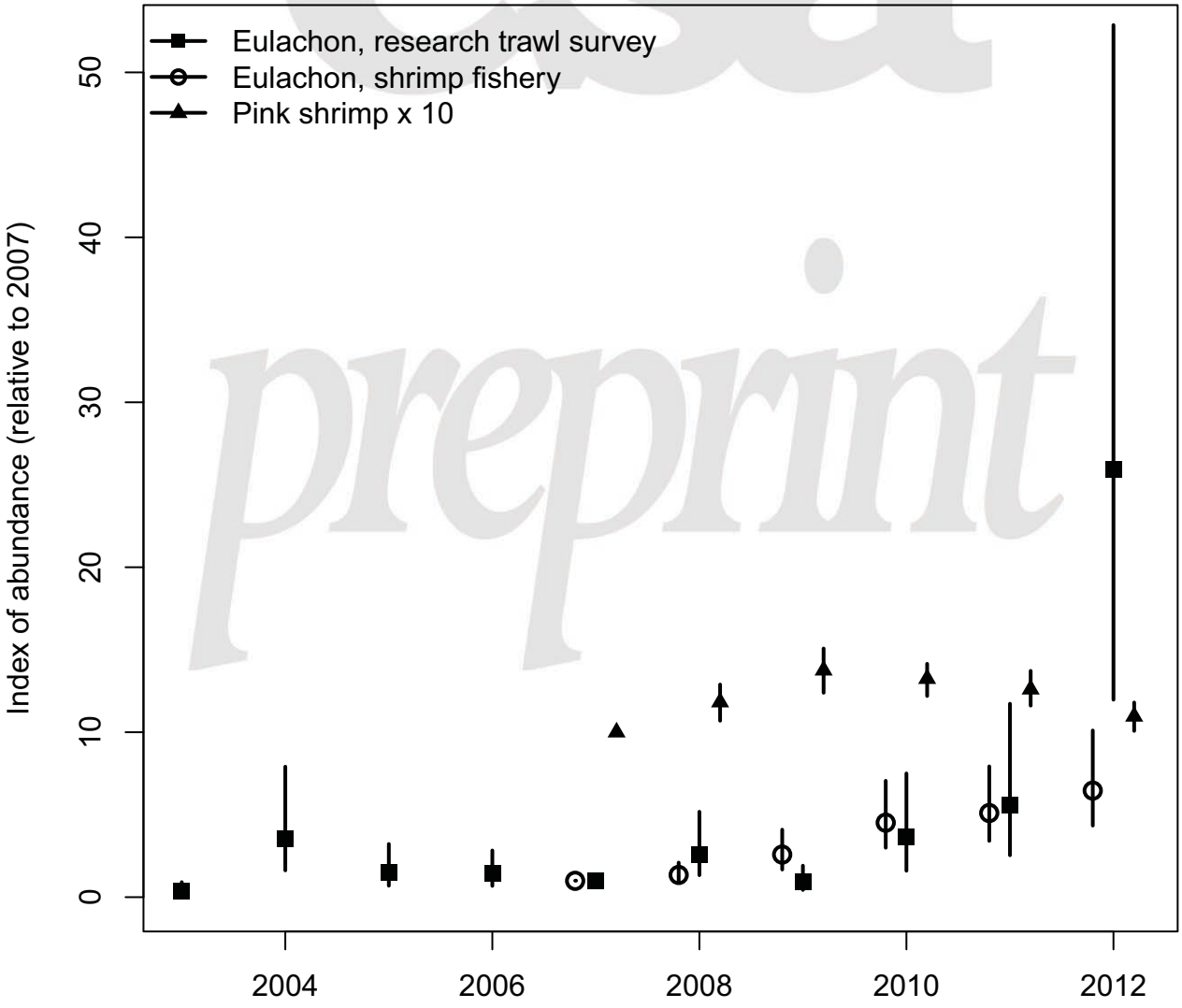

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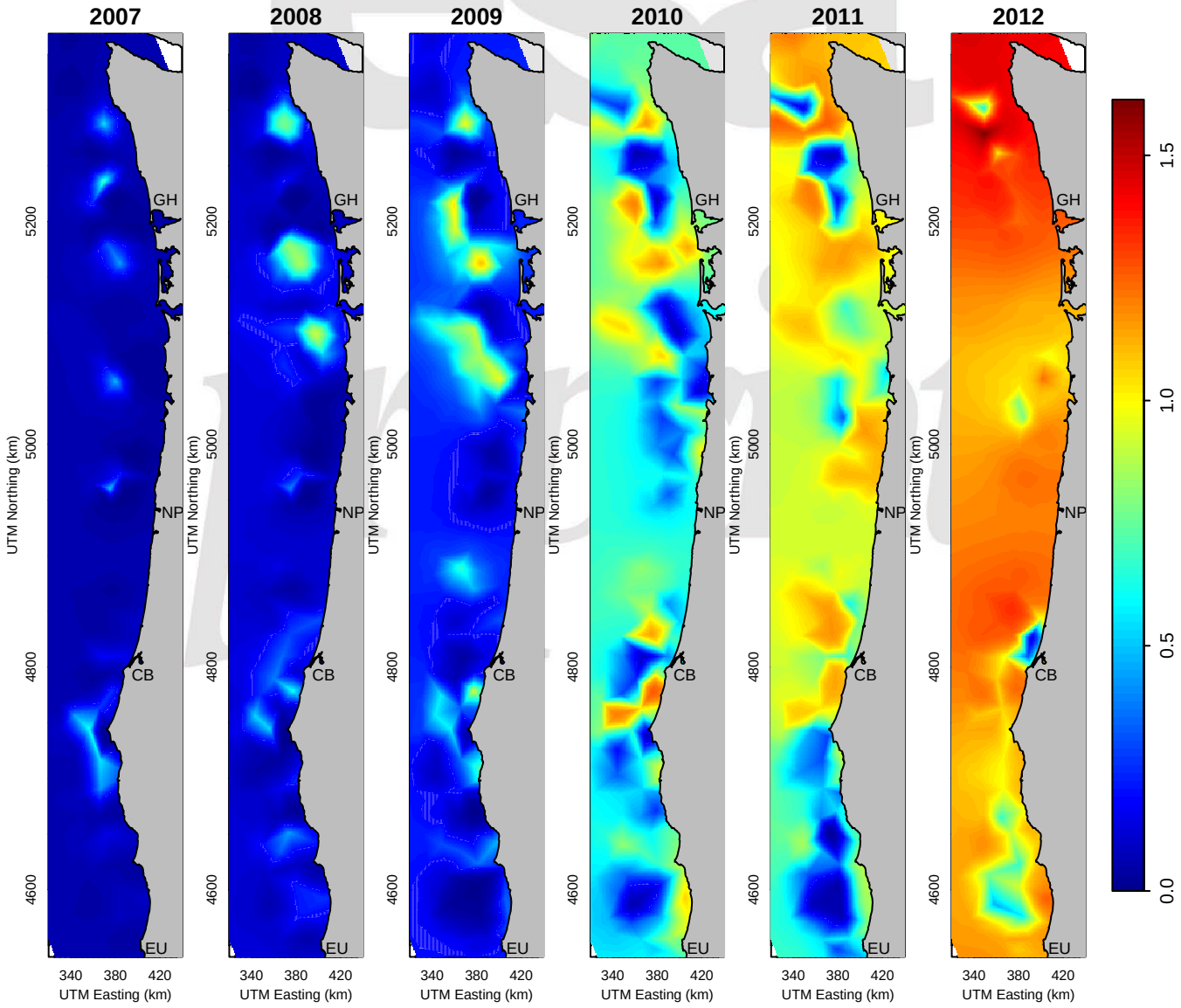

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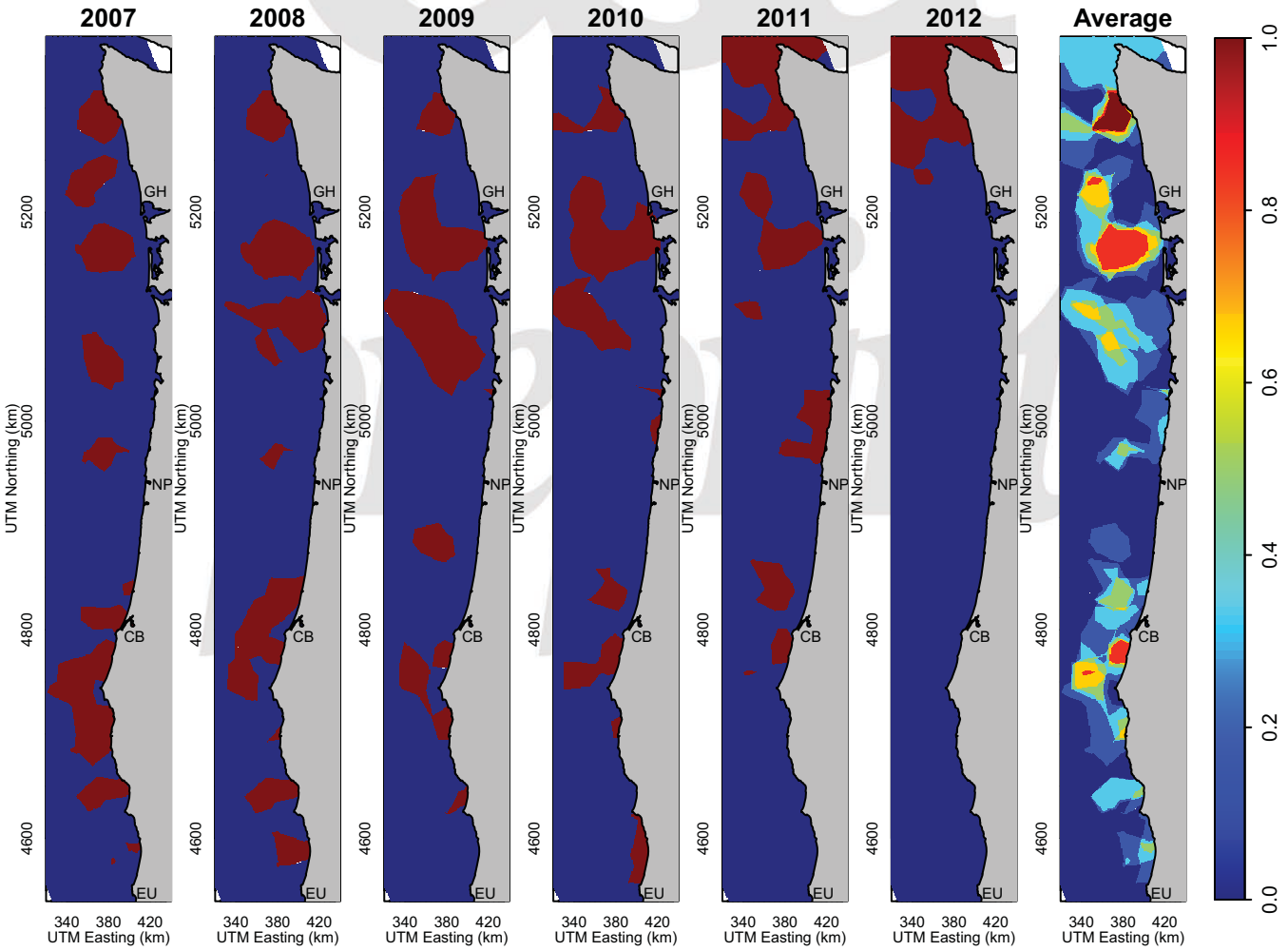

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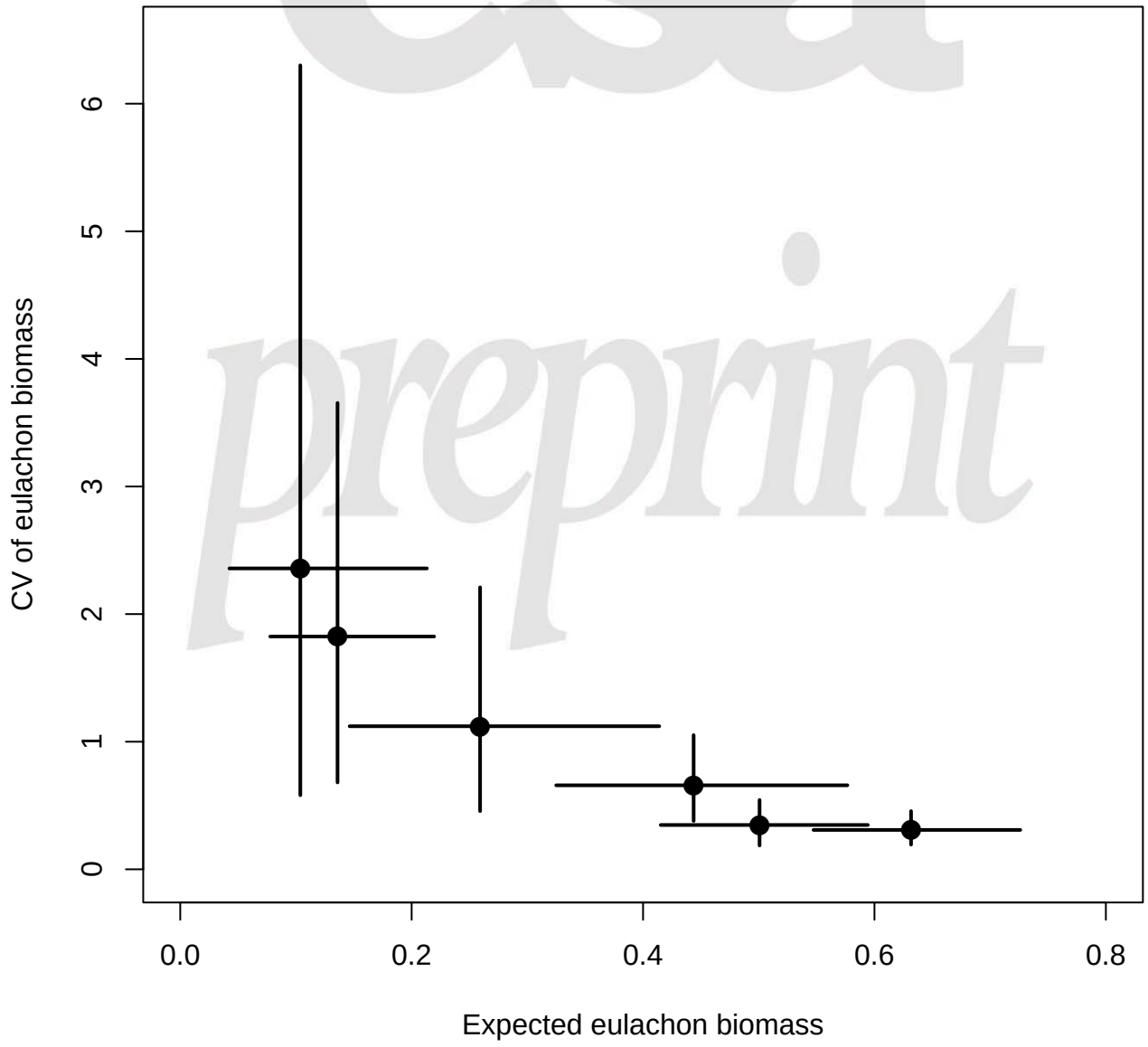

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