Bayesian change-point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary

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Abstract

We examined trends in abundance of four pelagic fish species (delta smelt, longfin smelt, striped bass, and threadfin shad) in the upper San Francisco Estuary (California, USA) over 40 years using Bayesian change-point models. Change-point models identify times of abrupt or unusual changes in absolute abundance (step changes) or in rates of change in abundance (trend changes). We coupled Bayesian model selection with linear regression splines to identify biotic or abiotic covariates with the strongest associations with abundances of each species. We then re-fitted change-point models conditional on the selected covariates to explore whether those covariates could explain statistically trends or change-points in species abundances. We also fitted a multi-species change-point model that identified change-points common to all species. All models included hierarchical structures to model data uncertainties, including observation errors and missing covariate values. There were step declines in abundances of all four species in the early 2000s, with a likely common decline in 2002. Abiotic variables, including water clarity, position of the 2 psu isohaline (X2), and the volume of freshwater exported from the estuary, explained some variation in species' abundances over the time-series, but no selected covariates could explain statistically the post-2000 change-points for any species.

Keywords: Hierarchical Bayes, change-point, Sacramento-San Joaquin Delta, delta smelt, longfin smelt, striped bass, threadfin shad, upper San Francisco Estuary.

Introduction

Declines in ecological condition across large areas are increasingly common around the world (e.g. Sala et al. 2001; Palmer et al. 2008; Cunningham et al. 2009), reflecting the increase in scope and intensity of human land use during the past century. The condition of estuaries has declined as a result of changing levels of terrestrial, freshwater, and marine stressors, including toxicants, nutrient enrichment, reduction of freshwater inputs, commercial and recreational harvest, dredging, and invasions of non-native species (Lotze et al. 2006). The San Francisco Estuary (California, U.S.A.) experiences all of these stressors, and populations of many aquatic species have declined since intensive human activities began in the mid 1800s (Bennett and Moyle 1996, Brown and Moyle 2005).

The San Francisco Estuary is the largest estuary on the Pacific coast of North America and consists of four major regions: San Francisco Bay, the most seaward region; San Pablo Bay and Suisun Bay, two intermediate brackish regions; and the generally freshwater Sacramento-San Joaquin Delta (Delta) (Fig. 1). The Delta is at the core of a massive system of dams and canals that store and divert water from the estuary for agricultural, industrial, and domestic use in central and southern California (Nichols et al. 1986). The water diversion facilities export c. 30% of the freshwater flow into the Delta on average, although that percentage has exceeded 60% during many recent summers (Kimmerer 2004).

The social, economic, and ecological effects of freshwater flows and diversions throughout the San Francisco Estuary have received tremendous attention. About 25 million Californians and 12,000 km^2 of agricultural land rely on water diversions from the Delta. Annual agricultural revenue from California’s Central Valley, which accounts for about half of the production of fruits and vegetables in the United States, frequently approaches $15 billion. Regulations on water diversions, including standards for the position of the 2 psu (practical salinity units) isohaline (a measure of the physical response of the estuary to freshwater flow; Jassby et al. 1995), locally termed X2, have become increasingly stringent.

Conflicts over water management in the Delta have intensified because of the apparently precipitous decline in abundance of four species of pelagic fish [delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*)] since c. 2000 (Sommer et al. 2007). Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993 and the listing was revised to endangered under the California act in 2009. Recent litigation to protect the species resulted in court orders to halt water diversions temporarily (Wanger 2007a, b). Longfin smelt was listed as threatened under the California Endangered Species Act in 2009 and was proposed but declined for federal listing.

Analyses of existing data and new field investigations have identified various factors that may help to explain the declines, but the relative importance of these factors, particularly water diversions, is unclear (Sommer et al. 2007). Identification of the processes causing declines, and their relative effects, is critical because the solutions under consideration include major investments in infrastructure, changes in water management, and rehabilitation of species' habitats that collectively will cost billions of dollars. Although an experimental evaluation of potential drivers is impossible for a system of this size, multi-decadal sets of data exist on abundances of pelagic fishes and biotic and abiotic characteristics of their environment, allowing for a robust correlative analysis.

There is interest in determining whether the recent declines in species' abundances are the continuation of longer-term trends or more abrupt changes in population dynamics (Manly and Chotkowski 2006), which we refer to as ecological "change-points" (Beckage et al. 2007). If the latter, identifying when these changes occurred, and if and when similar changes have occurred previously, is an important step towards understanding their causes and possible mitigation. We define a change-point as a point in time when an abrupt change occurred in the functional relationship between the mean abundance of a species and time. A change-point may be either a step change, which is an abrupt change in abundance; a trend change, which is an abrupt change in the temporal trend in abundance; or both.

There have been previous attempts to explore abrupt shifts in abundance trends of pelagic fish species in San Francisco Estuary. Manly (2005a, b) used log-linear models to examine whether a presumed step change in 2002 was statistically significant for several species, including the four we consider here. Manly and Chotkowski (2006) used a bootstrap approach to explore the timing of one or more change-points in the abundance of delta smelt. No method has been applied to detect objectively multiple change-points for all four species, whether individually or as a group. Neither has there been a rigorous examination of factors that might explain statistically specific change-points.

Here, we characterize abundance trends of delta smelt, longfin smelt, striped bass, and threadfin shad over the period of record (1967 to 2007), identify change-points for species individually and collectively, and examine whether biotic and abiotic covariates are related to those trends or change-points. To identify statistically the number, timing, and magnitude of any changes in abundance trajectories, and to integrate uncertainties into parameter estimates and inference, we constructed models based on Bayesian change-point techniques (Beckage et al. 2007). We used hierarchical model structures to separate explicitly observation error from natural process variation, to handle missing data, and to fit a multi-species change-point model. Hierarchical Bayesian models are ideally suited to the complexity of analysing ecological time-series (Webb and King 2009) because they can integrate multiple sources of information and uncertainty to provide more robust inferences about parameters and processes of interest (Cressie et al. 2009).

Biological background

Delta smelt are endemic to the San Francisco Estuary. They reach 60-70 mm standard length (SL), feeding throughout their life on mesozooplankton (Bennett 2005). Delta smelt are weakly anadromous. Upstream migration begins in mid-December and spawning occurs from March through May in freshwater. Most delta smelt spawn 12 to 15 months after birth. A small percentage live 2 years, possibly spawning in one or both years (Bennett 2005). Young delta smelt move downstream in early summer and remain in the low-salinity zone (0.5-10 on practical salinity scale) until they migrate for spawning.

Longfin smelt also are native to the San Francisco Estuary. Longfin smelt reach 90-110 mm SL with a maximum size of 120-150 mm SL (Moyle 2002; Rosenfield and Baxter 2007). Longfin smelt are anadromous. They spawn at age-2 in freshwater in the Delta from approximately December to April. Young longfin smelt occur from the low-salinity zone seaward throughout the estuary and into the coastal ocean. Longfin smelt feed on copepods as larvae and primarily on mysids as juveniles and adults.

Striped bass was deliberately introduced to the Delta from the east coast of the United States in 1879, and now supports a popular sport fishery (Moyle 2002). Striped bass is a large (> 1 m), long-lived (> 10 years) anadromous species. Females begin to spawn at age-4 in the Sacramento River, and to a lesser extent in the San Joaquin River, from April through June. Their semi-buoyant eggs hatch as they drift with the current. The larvae drift into the low-salinity zone where they grow, later dispersing throughout the estuary. Adults occur throughout the estuary to the coastal ocean, except during spawning migrations. Age-0 striped bass feed mainly on copepods, later switching to macroinvertebrates and then to fish.

Threadfin shad was introduced into California reservoirs as a forage fish in 1954 and eventually spread to the Delta (Moyle 2002). Adult threadfin shad are typically <100 mm total length and primarily inhabit freshwater. They switch between filter-feeding and particle feeding, consuming phytoplankton, zooplankton, and detritus. Most threadfin shad spawn in their second summer of life, although some may spawn at the end of their first year. Spawning occurs mainly in June and July. Threadfin shad is the most abundant pelagic fish in the upper San Francisco Estuary and is important as prey for piscivorous species.

Statistical analyses

We used a Bayesian framework to fit a series of log-linear models to explore temporal patterns in species abundances and relationships with biotic and abiotic covariates. First, we used piecewise regression models (Denison et al. 1998, Fernhead 2006) to characterize temporal trends in abundance of each species and to identify change-points in either the absolute abundance (step changes) or in the rate of change in abundance (trend changes). Next, we used Bayesian model selection (Green 1995) to identify covariates with the strongest associations with abundances of each species. We then fitted change-point models conditional on the selected variables to explore whether those covariates could account statistically for changes detected by the trend model, or lead to detection of other change-points. We also fitted a multi-species change-point model to determine whether there were years in which all species collectively experienced abrupt changes in abundance not explained by the selected covariates.

Hierarchical log-linear trend models

For each species, we fitted a log-linear trend model using piecewise linear splines (Denison et al. 1998) that allow for changes in the intercept or slope parameters at particular times (i.e. change-points). We used a hierarchical model to account explicitly for sampling error. For each species, the observations (y_t) were the mean number of individuals captured during autumn trawl surveys conducted each year from 1967 to 2007 (Stevens and Miller 1983). The mean for each year was based on monthly (September, October, November, December) samples from 100 different locations; thus, the yearly average was based on c. 400 observations (data and station details available at http://knb.ecoinformatics.org/knb/metacat/nceas.958.8/nceas/). We assumed that the observations were unbiased estimates of the true mean abundance (n_t) in a standard trawl sample over the four-month period in year t and that the 100 sampling stations are an adequate spatial representation of the estuary. The resulting hierarchical model for observations and true abundances was:

$$y_t \sim Normal(n_t, \sigma_{Ot}^2), \qquad (1)$$
$$n_t \sim LogNormal(\alpha_t + f_t(t), \sigma_p^2). \qquad (2)$$

Simultaneously estimating observation noise, σ_{Ot}, and process variation, σ_p, is difficult for such hierarchical models (e.g. Dennis et al., 2006). Therefore, we substituted the observed standard errors of trawl samples as estimates of σ_{Ot} in the fitting procedure.

The parameters of the state process model, α_t and $f_t(t)$ in equation (2), allowed for abrupt changes in the (log) abundances and changes in the relationship between abundance and time, respectively. The following submodel accounted for abrupt changes to the intercept, or step changes:

$$\alpha_t = \alpha_1 + \sum_{j=1}^{k_\alpha} \chi_j I(t \geq \delta_j) \qquad (3)$$

In this submodel, α_1 is the initial log abundance of a given species, k_α is the number of step changes in abundance, δ_j is the timing of the j^{th} step change, and χ_j is the value of the change. $I(t \geq \delta_j)$ is an indicator function that equals 1 when $t \geq \delta_j$ and is 0 otherwise. To illustrate, we present an example of the state process model (2) fitted to abundance data with a single step change and constant linear trend (Fig. 2a).

We modeled the temporal trend, $f_t(t)$, as a piecewise linear regression with an unknown number k_β of changes in slope (trend changes) and a corresponding set of times θ_j of trend changes, or “knots” (Harrell 2001).

$$f_t(t) = \beta_1 t + \sum_{j=1}^{k_\beta} \beta_{[j+1]}(t - \theta_j)_+ . \qquad (4)$$

The term $(t\text{-}\theta_j)_+$ equals $I(t \geq \theta_j)(t\text{-}\theta_j)$. Given a particular intercept, the term $f_t(t)$ is a piecewise linear and continuous function of time, but when the intercept α_t varies, the combination $\alpha_t + f_1(t)$ is a discontinuous piecewise linear model (Fig. 2b).

Given uncertainty about when or if step or trend changes occurred, we treated the numbers, k_α and k_β, and timing, δ_j and θ_j, of change-points as unknown parameters to be estimated as part of the model. We used a Bayesian framework with reversible jump Markov chain Monte Carlo sampling (MCMC, Lunn et al. 2006, 2008) to evaluate the posterior model probabilities (i.e. evidence) for all possible models, or combinations of change-points. The range of models considered possible is specified in the prior distributions, which are detailed below. The resulting posterior distributions allow for probabilistic inferences about the occurrence of change-points in particular years, accounting for uncertainties in both data and other model parameters (including magnitudes and timing of other change-points). The posterior probability that a change-point occurred in year y is the summed posterior probabilities of all models that include a change-point in year y (e.g. of all values of δ that include y as an element).

Prior distributions for parameters.

In Bayesian analysis, prior distributions must be specified for the unknown parameters (Gelman et al. 2004). Our prior distributions limited the number of step and trend changes to a maximum of four each, and included the possibility of zero change-points: k~Binomial(4,0.5). This prior reflects our expectation that, in a system subjected to increasing anthropogenic influence over the period of record, there may have been multiple changes in abundance trends. The prior explicitly limits the number of change-points so the larger and more abrupt changes are highlighted (see Appendix A for further discussion of priors). The priors were uninformative with respect to the timing of change-points, with equal prior probability [$p_0 = (0.5\times4)/39 = 0.05$] of change-points in each year (Appendix A). With this prior, a posterior probability $p_1 > 0.14$ for a change-point in year y corresponds to an odds ratio of 3, which is a threefold increase from the prior odds [$p_0/(1- p_0)$] to the posterior odds [$p_1/(1- p_1)$]. Odds ratios are measures of the evidence in the data in favor of one hypothesis (change-point in year y)

over an alternative (no change-point in year y), and values > 3 are generally considered to indicate "substantial" evidence (Jeffreys 1961).

We specified normal prior distributions with zero mean and standard deviations equal to $(\ln y_{max} – \ln y_{min})/1.96$ and $0.25 \times (\ln y_{max} – \ln y_{min})/1.96$ for the magnitude of step (χ) and rate (β) changes, respectively. These priors imply that step changes greater than the observed data range are unlikely (prior probability < 0.05) and that the greatest change in slope in one year is unlikely to be greater than one-quarter of the range of log values of the observed data. We used several uninformative prior distributions for the unknown parameters (numbers and magnitudes of change-points) to assess sensitivity to the choice of priors (Appendix A). Although absolute values of model posterior probabilities sometimes were sensitive to choice of priors, the relative probabilities, and hence inferences about change-point times, were consistent.

Covariate effects

We undertook a series of steps to identify biotic or abiotic variables that may explain temporal patterns in species' abundances and to determine how those variables affected inferences about change-points. First, a set of Q (12 to 15) candidate covariates was selected for each species on the basis of previously published work and unpublished analyses (Table 1). Next, we used Bayesian model selection to identify which of the Q candidate variables had the strongest associations with variation in the (log) abundances of each species (see *Variable selection model*, below). We then fitted change-point models conditioned on the selected variables by replacing the trend component $f_t(t)$ in equation (2) with covariate effects $f_x(X)$. These *covariate-conditioned change-point* models identify abrupt changes in abundance that would not be expected given the covariate values and estimated species-covariate relationships. Changes in species' abundance that are identified as change-points in covariate-conditioned models are unlikely to be related to the included covariates. But if the inclusion of a covariate reduces the evidence for a previously identified change-point (i.e. one identified in a trend model or model conditioned on other covariates), then a causal relationship between that covariate and the change-point is plausible.

Variable selection model

The variable selection model allowed non-linear covariate effects and temporal autocorrelation. Covariates were standardized (mean 0, SD 1) prior to model fitting and missing values were assigned normal prior distributions, which were not updated during model fitting, with mean 0 and SD 1. The model was:

$$n_t \sim Lognormal\left(\alpha + \sum_{j=1}^{Q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt}-\phi_{jm})_{+} + \rho\log n_{t-1}, \sigma_p^2\right). \qquad (5)$$

This model has up to Q covariates with effects fitted as piecewise linear splines with k_j slope parameters $\boldsymbol{\beta}_j$ and free knots $\boldsymbol{\phi}_j$. If $k_j = 0$, variable j has zero effect; if $k_j = 1$, variable j is included as a linear effect (for $x_j > \phi_{j1}$); and if $k_j > 1$, variable j is included as a non-linear effect. We used a categorical prior for k_j such that the prior probabilities of values 0, 1, 2, and 3 were 0.5, 0.3, 0.1, and 0.1, respectively. Thus, the prior probability that variable j was included in the model, Pr($k_j > 0$), was 0.5, and linear effects were more probable a priori than were non-linear effects. The knots were assigned uniform discrete priors with 10 possible positions evenly spaced along the range of x_j.

The relative importance of each of the covariates in model 5 was measured by the posterior probability of inclusion for each variable, Pr($k_j > 0$), which is the sum of the posterior model probabilities of all models that include a particular variable. We considered Pr($k_j > 0$) > 0.75, corresponding to an odds ratio of 3 [(0.75/0.25)/(0.5/0.5)], to be sufficient evidence to include variables in subsequent covariate-conditioned change-point models.

With all models (combinations of variables) equally probable a priori (prior $\Pr(k_j > 0) = 0.5$), posterior model probabilities reflect differences in marginal likelihoods, which intrinsically penalize model complexity (Kass and Raftery 1995; Beal et al. 2005). The amount of penalty depends on the prior distributions for model parameters (more diffuse priors favor fewer model parameters, George and Foster 2000), so posterior model probabilities, hence $\Pr(k_j > 0)$, can be sensitive to the choice of priors. We used a half-Cauchy prior (Gelman 2006) for the standard deviation σ_β of non-zero covariate effects, scaled so that c. 90% of the resulting prior probability mass of each linear coefficient β_{jm} was in the interval (-1,1) and 95% was in the interval (-2,2). This prior placed most weight on more plausible coefficients (a linear coefficient of 1 equates to a 2.7-fold change in abundance for 1 SD change in the predictor) while still allowing larger effects (e^2 = 7.4-fold change in abundance per 1 SD change in predictor). We also fitted models with a range of alternative prior specifications and generally obtained similar results (Appendix A). Any variables for which $\Pr(k_j > 0)$ values were sensitive to priors are identified in Results.

We fitted the variable selection model (equation 5) with and without the autocorrelation term ρn_{t-1} ,and with a conditional prior on ρ [$\rho | k_{Q+1}=1 \sim \text{Normal}(0, \sigma_\beta^2)$; $k_{Q+1} \sim \text{Bernoulli}(0.5)$] testing for the importance of the autocorrelation term (i.e. treating n_{t-1} as a candidate predictor). $\Pr(k_j > 0)$ values for covariates were largely unaffected by the treatment of ρ, so we present results only for the models that treated n_{t-1} as a candidate predictor.

Covariate-conditioned change-point model

We fitted change-point models that accounted for the effects of covariates identified as probable predictors [those with $\Pr(k_j > 0) > 0.75$] to examine whether those covariates could account for changes detected by the trend model, or detect other change-points. The covariate-conditioned change-point model with $q < Q$ covariates was:

$$n_t \sim Lognormal\left(\alpha_t + \sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt}-\phi_{jm})_{+} + \rho\log n_{t-1}, \sigma_p^2\right). \qquad (6)$$

In this model, k_j had minimum value = 1 and a prior distribution given by $k_j = 1 + \kappa_j$, where κ_j~Binomial(3,0.3), the first knot ϕ_{j1} was fixed at min(x_j), and remaining knots had continuous uniform priors. The autocorrelation term was included only if results of the variable selection model indicated that ρ probably was non-zero (i.e. when Pr(k_{Q+1}=1)>0.75) [n.b. we confirmed that including ρ when Pr(k_{Q+1}=1) < 0.75 had no effect on other parameters in equation 6].

In equation (6), the covariate effects $\sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt}-\phi_m)$ replace the trend component $f_t(t)$ in equation (2). Including step change(s) in the intercept allowed for abrupt changes in abundance conditional on the covariates, that is, changes that would not be expected given the covariate values and estimated species-covariate relationships (Fig. 2c). If a step change in n_t was explained by a step change in the covariate, then the model intercept would remain constant (i.e. no change-point, Fig. 2d).

Multi-species model

We searched for common change-points among species by fitting covariate-conditioned change-point models [equation (6)] for all species simultaneously, with an additional step change submodel that was common to all species. In the multi-species model, the time-dependent intercept for species *s*, α_{st}, was modeled as:

$$\alpha_{st} = \alpha_{s1} + \sum_{j=1}^{k_{s\alpha}}\chi_{sj} I(t \ge \delta_{sj}) + \sum_{l=1}^{k_{C\alpha}}\psi_l I(t \ge \zeta_l). \qquad (7)$$

Here, $k_{C\alpha}$ is the number of step changes common to all four species, with magnitude and timing given by vectors ψ and ζ, respectively. The other parameters in equation (7) define species-specific change-points as in equation (3), with subscript *s* in (7) denoting species-specific parameters. The full model for each species was identical in all other respects to equation (6).

The multi-species model identified any year(s) in which abundances of all species changed unexpectedly given the values of relevant covariates. We fitted the model once with prior distributions that allowed only common change-points [$k_{s\alpha} = 0$, $k_{C\alpha} \sim$ Binomial(4,0.5)] and once with prior distributions that allowed both common and species-specific change-points [$k_{s\alpha} \sim$ Binomial(2,0.5), $k_{C\alpha} \sim$ Binomial(2,0.5)]. We also examined combinations of fewer species to determine whether results of the four-species models were overly influenced by one species.

Implementation

All models were estimated using the reversible jump MCMC add-on (Lunn et al. 2006, 2008) for WinBUGS v1.4 (Lunn et al. 2000) with 3 chains of 200 000 iterations each after 50 000 iteration burn-in periods. MCMC mixing and convergence were established by inspection of chain histories, autocorrelation plots, and Brooks-Gelman-Rubin statistics. We used the `cut()` function in WinBUGS (Lunn et al. 2000) to prevent updating the prior distributions for missing values, which otherwise may be tuned to fit the model, leading to selection of covariates with many missing values as predictors. This treatment of missing values allowed all available data to be used in the analysis, rather than omitting years in which any covariate values were missing (Carrigan et al. 2007). We did not use imputation methods to estimate missing values because these methods assume values are missing at random, which generally was not the case (e.g. values for the first six years of surveys were missing for some variables).

WinBUGS code for all models is available in Supplementary material.

Results

Overview of results relevant to recent declines

The trend models identified probable step or trend changes in the early 2000s for delta smelt (trend change 2000-2002, Fig. 3A), striped bass (step decline 2002, Fig. 4A), and threadfin shad (step decline 2002, Fig. 5A). Longfin smelt abundances also declined after 2000, but this decline was modeled as a continuation of a long-term declining trend that was interrupted by sudden increases in the late 1970s and mid 1990s (Fig. 6A).

The species-specific, covariate-conditioned change-point models indicated step declines in abundances (i.e. abrupt declines that could not be modeled by the included covariates) of delta smelt and longfin smelt in 2004 (Figs. 3B and 6B) and of striped bass (Fig. 5B) and threadfin shad (Fig. 6B) in 2002.

In the multi-species change-point models, there was strong evidence of a common change-point in 2002, regardless whether species-specific change-points were allowed (Fig. 7). Evidence for step declines in abundance of delta smelt and longfin smelt in 2004 remained in the multi-species model that allowed species-specific change-points (Fig. 7). Similar results were obtained from multi-species models fitted with any combination of three species, so the high probability of a common change-point in 2002 is not driven by any single species.

To ensure that our variable selection criterion [$\Pr(k_j > 1) > 0.75$] had not excluded variables that could explain the post-2000 declines, we refitted covariate-conditioned change-point models including all variables with $\Pr(k_j > 1) > 0.5$ (i.e. variables with some evidence of effects). We also fitted models with variables that had strong effects in a multivariate autoregressive (MAR) analysis of an expert-elicited model of this system (up to 6 variables per species, see Mac Nally et al. in review for details). With one possible exception (detailed in *striped bass* results, below), inclusion of additional variables had no substantive effects on posterior probabilities of post-2000 change-points in single- or in multi-species models.

Water clarity emerged as a likely predictor of the abundance of delta smelt, longfin smelt, and striped bass, but the other variables with Pr(k_j > 1) > 0.75 were unique to each species (Table 2). No species had more than two variables with Pr(k_j > 1) > 0.75. All of the covariates with Pr(k_j > 1) > 0.75 had monotonic effects, and most were modeled adequately by a single linear coefficient ($k_j = 1$).

The autocorrelation coefficient, ρ, had low probability of inclusion [low Pr(k_{Q+1}=1)], and was close to zero when included, for all species except striped bass (Fig. 3C, 4C, 5C, 6C, Table 2). Low values of ρ may indicate that the mean abundance from September through December is poorly correlated with abundance of spawning adults in a given year.

Species-specific results

Delta smelt. – In the variable-selection model for delta smelt, water clarity and winter exports had high probability of inclusion [Pr(k_j > 1) > 0.75)] (Fig. 3C). Both variables had negative effects (Table 2). The effect of winter exports was approximately linear, but marginal effects of water clarity were greatest at high values. The probability of inclusion for winter exports was sensitive to the prior distribution specified for linear coefficients. Priors that weighted large effect sizes (e.g. absolute linear coefficients > 0.5) more heavily yielded low Pr(k_j > 0) values for winter exports. This sensitivity indicates that the data support relatively small effects of winter exports ($|\beta| < 0.5$), but models with larger export coefficients fitted the data poorly. The estimated mean linear coefficient in the step change model (β = -0.25, Table 2) implies that one standard deviation increase in volume of winter exports (= 0.62 km^3) would be associated with a 22% decline (95% posterior interval = - 45% to +9%) in abundance of delta smelt, assuming other factors were constant.

Evidence for change-points in the periods 1981-1983 and 2000-2002 was weaker in the covariate-conditioned model (Fig. 3B) than in the trend model (Fig, 3A), suggesting that those declines in abundance may have been associated with combined effects of increasing water clarity and high winter exports (Fig. 8). However, there was evidence of an unexplained decline in 2004 in the single-species model (Fig. 3B), and of unexplained declines in 2002 and 2004 in the multi-species model (Fig. 7A). The mean effect of winter exports was slightly less negative in the multi-species model than in the single-species model (Table 2) because the multi-species model assigned more weight to an unexplained step decline in 2002, reducing the estimated effect of high winter exports in that year.

Longfin smelt. – In the variable selection model for longfin smelt, water clarity and spring X2 had high probability of inclusion [$\Pr(k_j > 1) > 0.75$)]. Both variables had negative effects that were approximately linear (Fig. 6C, Table 2).

The change-point model conditioned on spring X2 and water clarity indicated unexpected declines in abundance from 1989 to 1991 and in 2004 (Fig. 6B). The sharp increases in longfin smelt abundance in 1978 and 1995, identified as step increases in the trend model, were modeled as responses to sharp declines in X2 (increases in outflow; Fig. 8) in the covariate-conditioned change-point model. The estimated relationship between water clarity and longfin smelt abundance was weaker in the single species change-point model than in the multi-species change-point model (Table 2). This disparity relates mainly to differences in the way the models explained abundance from 1988 through 1992. A sharp decline in longfin abundance in that period was largely modeled as an unexplained step decline in the single-species model but, when species-specific change-points were given lower prior probability in the multi-species model, that decline was partially attributed to increasing water clarity (Fig. 8). If change-points were omitted, as in the variable-selection model, the water clarity effect was very strong. These results suggest that the relationship between longfin smelt abundance and water clarity, after accounting for a strong effect of spring X2, generally was weak throughout the time series, and that the strong relationship identified in the variable selection model was driven largely by data for the period 1988 through 1992.

Striped bass (age-0). – In the variable selection model for striped bass, water clarity and the autocorrelation term had $\Pr(k_j > 1) > 0.75$. Water clarity had an approximately linear negative effect (Table 2).

Evidence for a step decline in striped bass abundance in 2002 was lower in the covariate-conditioned change point model (Fig. 4B) than in the trend model (Fig. 4A), and was lower still (odds ratio < 3) in a model that included the biomass of inland silverside (*Menidia beryllina*) ($\Pr(k_j>0) = 0.59$, Fig. 4C). These results suggest that high water clarity (Fig. 8) or biomass of inland silverside could have contributed to the 2002 step decline in striped bass abundance. However, the presence of partial autocorrelation ($0 < \rho < 1$) complicated change-point detection in these log-linear models because the interpretation of α, and hence appropriate prior distributions for change-points, depends on ρ (see Appendix A). When autocorrelation was omitted from covariate-conditioned, change-point models for striped bass, regardless of the inclusion of inland silverside biomass, the posterior probability of a step change in 2002 was > 0.4 (Fig. 4B).

In all covariate-conditioned models for striped bass, relatively low water clarity in 1981 accounted for the apparent step increase in abundance in that year (Fig. 4A vs 4B and 7C).

Threadfin shad .– No variables had high probability of inclusion in the threadfin shad variable selection model. The highest-ranked variables, other than the autocorrelation term, were biomass of summer calanoids in the low salinity zone and winter and spring export volumes, which each had posterior probability of inclusion marginally higher than the prior probability (Fig. 5C), indicating only weak evidence of effects. However, probabilities of inclusion for winter and spring exports were sensitive to the prior distribution for the linear coefficients, and priors that put more weight on smaller coefficients yielded $\Pr(k_j > 1) > 0.75$ for both variables; no other variables showed this level of sensitivity to priors. Therefore, we included winter and spring exports in covariate-conditioned change-point models for threadfin shad. We also included time as a covariate in the single-species model for threadfin shad because the model with export volumes alone fit too poorly (R^2 = 0.33) to make meaningful inferences about change-points (i.e. unusual departures from “expected” abundance given covariate values).

The estimated relationship between log abundance of threadfin shad and spring exports was similar in form and magnitude to the relationship between log abundance of delta smelt and winter exports (Table 2), and was consistent among single- and multi- species models with and without time included as a covariate. An apparent step increase in threadfin shad abundance in 1977 (Fig. 5A) was modeled as a response to low spring exports in that year (Fig. 8) in the covariate conditioned models (note near-zero change-point probabilities for 1977 in Fig. 5B and 7D). The estimated relationship between winter exports and threadfin was weak in all models (Table 2), especially in the multi-species model that weighted 2002 step changes more heavily. The inclusion of summer calanoid biomass and an autoregressive term [both variables had $0.5 < Pr(k>0) < 0.75$] had no effect on posterior probabilities of change-points for threadfin shad (estimated coefficients were close to zero in both cases).

Discussion

Different model structures, particularly models for individual species compared with multiple species, yielded somewhat different sets of the more likely change-points, but all models indicated sharp declines in abundance of delta smelt, longfin smelt, threadfin shad, and striped bass in the early 2000s. Post-2000 change-points were evident in all covariate-conditioned models for all species, indicating that the covariates identified as the strongest predictors of abundance could not explain fully the recent declines. However, there was some evidence that increasing water clarity, winter exports, and spring X2 may have contributed to post-2000 declines in abundance of some species.

Inferences about declines in abundance after 2000 depend partially on whether species were considered jointly or separately. When delta smelt and longfin smelt were modeled individually, the best-supported models largely associated the 2002 decline in abundance of delta smelt with high winter exports and the 2001 decline in abundance of longfin smelt with spring X2. In these models, sharp, unexplained declines in abundance did not occur until 2004. However, in the multi-species model all four species experienced unexplained declines in 2002, and the estimated effects of winter exports and spring X2 on delta smelt and longfin smelt, respectively, were moderately reduced (Table 2). A similar reduction in the estimated effect of winter exports in the multi-species model was observed for threadfin shad. The increased probability of unexplained declines in 2002 and reduced covariate effects in the multi-species model, relative to the single-species models, reflect differences in the amounts of data (evidence) used to fit the different models. Combining evidence from all species in the multi-species model strengthened the case for an unexplained (by the covariates considered) step decline in 2002 for all species, and led to a corresponding reduction in the estimated influence of variables that, in single-species models, might have explained 2002 declines for individual species. These results are consistent with a hypothesis that simultaneous, abrupt declines in abundances of multiple species are more likely to have been caused by a common, but unknown, factor than by different factors for each species (e.g. winter exports for delta smelt and threadfin shad, spring X2 for longfin smelt, another unknown factor for striped bass).

The covariate-conditioned models indicated step declines in abundance of age-0 striped bass in 1987 (evident in a model without autocorrelation) and step declines of longfin smelt in 1989 to 1991. These declines may be related to the effects of the introduced (c. 1987) clam *Corbula amurensis*, which caused an ongoing decrease of c. 60% in chlorophyll *a* concentration in the estuarine low-salinity zone (Alpine and Cloern 1992). There were concurrent declines in abundance of mysids and some species of copepods upon which striped bass and longfin smelt prey (Kimmerer and Orsi 1996, Orsi and Mecum 1996, Kimmerer 2006). These changes in prey abundance were evident in the diets of striped bass and other fish species (Feyrer et al. 2003). Although variable-selection models did not identify prey variables as strong predictors of fish abundances at the whole-estuary scale of this analysis, summer calanoids and mysid biomass were positively correlated with abundances of striped bass and longfin smelt (calanoids only) in a multivariate autoregressive (MAR) model of this system (see Mac Nally et al., this issue). When those prey variables were included in covariate conditioned models for striped bass, evidence for an unexplained step decline in 1987 was reduced greatly (to odds ratio < 3), supporting the prey-availability hypothesis. Conversely, the inclusion of prey biomass did not alter substantially evidence for step declines in 1989 and 1991 in longfin smelt abundance.

Covariate relationships and previous analyses

The covariates we identified as strongly associated with pelagic fish abundance, namely X2, water clarity, and export flows, previously have been hypothesized to affect abundance. Jassby et al. (1995) and Kimmerer (2002) identified a relationship between abundances of several species of estuarine-dependent nekton and freshwater flow indexed as spring X2. An association between abundance of striped bass and X2 has been identified before, but the relationship with X2 was weaker than for longfin smelt and the relationship was affected by other factors (Jassby et al. 1995, Kimmerer 2002, Kimmerer et al. 2008). In these previous studies, X2 did not strongly affect the autumn abundance of delta smelt or threadfin shad. These results are consistent with our result that only longfin smelt had a strong (and negative) relationship with spring X2 (Table 2).

The association between water clarity and abundance that we identified also is consistent with previous analyses. Water clarity can affect composition of fish assemblages in large river and estuarine systems (Blaber and Blaber 1980, Quist 2004) and can mediate predator-prey interactions (Abrahams and Kattenfeld 1997, Gregory and Levins 1998). Water clarity (measured by Secchi disc depth) has been related to distributions of several species of fish in the San Francisco Estuary. Delta smelt and striped bass, but not threadfin shad, were most likely to occur where water was turbid during autumn (Feyrer et al. 2007). Secchi depth also explained some of the variation in distribution of delta smelt in summer (Nobriga et al. 2008). Adding Secchi depth to non-linear models of distribution based on salinity improved fits substantially for delta smelt, striped bass, and longfin smelt (Kimmerer et al. 2009). These effects of water clarity on distributions may translate to effects on abundance to the extent that the fish populations are limited by the availability of habitat. Laboratory experiments and observations suggest that young delta smelt cannot feed effectively unless particles are suspended in the water column (Baskerville-Bridges et al. 2004; Mager et al. 2004).

Export flows in winter and spring were negatively associated with abundance of delta smelt and threadfin shad, respectively, in our models. Previous analyses indicated that export flows can remove a substantial fraction of the delta smelt population in both winter and spring of dry years (Kimmerer 2008). Although previous analyses reported an effect of export flows on the abundance of young striped bass (Stevens et al. 1985), this effect was negligible if egg supply was taken into account (Kimmerer et al. 2001). Threadfin shad has been abundant relative to other species in freshwater zones of the Delta since monitoring began (1967). However, the proportional loss of the threadfin shad population to export operations has not been determined. Of the four species we examined, only threadfin shad occupies the freshwater portion of the Delta for its entire life cycle. The other three species move into brackish water during summer and autumn. Given that water diversions only export freshwater, threadfin shad may have been especially vulnerable to exports throughout the year.

The variable-selection results suggest that, at the estuary scale, abiotic factors (water clarity, X2, exports) may have more influence on interannual variation in abundances of the four species than do biotic variables. This result is consistent with a multivariate autoregressive (MAR) analysis of an expert-elicited model of this system that included species interactions among several trophic groups as well as abiotic covariates (Mac Nally et al, this issue). In the MAR analysis, abiotic variables explained 50% more variation than did trophic interactions.

Trophic interactions were still important (Mac Nally et al., in review), but the strongest effects generally were “top-down,” with fish apparently having more influence on prey biomass than vice versa. These results suggest that targeted manipulation of abiotic variables like water clarity, freshwater flow, and water exports could be used to influence fish abundances in this system, but greater understanding of the interactions between abiotic variables and trophic interactions is required before scientifically robust management alternatives can be formulated. Identification of the factor(s) that caused the post-2000 declines remains an important challenge – attempts to reverse declines are unlikely to succeed unless the main drivers of those declines are understood. Our results confirm that the four species of pelagic fish experienced abrupt declines around 2002, and suggest that all potential drivers not considered in our analyses warrant further investigation.

Strengths of hierarchical Bayesian modeling

The hierarchical Bayesian modeling approach has several advantages over other approaches, such as multiple regression models (Cressie et al. 2009). The hierarchical structure allows sampling or measurement error to be separated from actual variation in underlying abundances, which can improve estimation of the underlying biological processes (Clark 2005). Hierarchical Bayesian models allow considerable flexibility in modeling of biological processes, so a wide variety of process models can be formulated and fitted within a common framework. The availability of public domain software such as WinBUGS, combined with an add-on developed by Lunn et al. (2006) for reversible jump MCMC (Green 1995), makes it increasingly feasible to fit and compare complex hierarchical models within a consistent estimation framework. We examined non-parametric trend models with change-points for step and trend changes (eq. 2), non-linear variable selection models (eq. 5), non-linear covariate models with step changes (eq. 6), and multiple-response models (eq. 7), which all included temporal autocorrelation as appropriate. Within each of these general model classes were large sets of special cases that differed with respect to the particular change-points and covariate effects included. Many models of a given class were compared or combined for inference on the basis of marginal likelihoods, which inherently penalize model complexity. For example, the capacity to treat the number and location of “knots” (i.e. change-points) in linear splines as unknown parameters allowed the relative evidence for change-points in specific years to be evaluated by formal comparison of a very large number of possible models (all possible combinations of up to four change-points per parameter) while simultaneously estimating other parameters of interest (e.g. covariate effects) and accounting for data uncertainties (e.g. observation errors and missing covariate values).

Future work

Three areas of future research could help reduce uncertainty about drivers of abundance of pelagic fishes in the San Francisco Estuary. One is to pursue, in greater depth, simultaneous modeling of multiple species and interactions among species and covariates. The multiple-species change-point models did not consider interactions among the four species of interest (but see Mac Nally et al. in review), and interactions among covariates were not investigated. Some preliminary work (J. R. Thomson, *unpublished results*) fitting Bayesian additive regression trees (BART, Chipman et al. 2008) included interactions among covariates, but initial results did not yield substantial improvements in fits, and the post-2000 declines were not modeled adequately.

Another area of future work that may clarify mechanisms is to fit process models that include multiple life-history stages of the fish species using data available from surveys that complement data from autumn midwater trawl surveys used here. For example, adult delta smelt are sampled from January through April throughout the estuary with a Kodiak trawl (a surface-oriented trawl), and small juveniles are sampled from March through July in the “20-mm survey” (Dege and Brown 2004). In summer, juvenile delta smelt are sampled with tow-net surveys. A life history model that linked the abundances of each life stage would provide a more continuous picture of the delta smelt population and would capitalize more fully on available data. The approach to change-point identification used here could be applied to any parameter(s) of interest (e.g. population growth parameters) within almost any model structure (Lunn et al. 2006), which may allow identification of important changes in key processes.

A third potential means to elucidate drivers of abundance is to carry out formal statistical comparisons of some of the models formulated by Sommer et al. (2007) and Baxter et al. (2008) to explain declining abundances of pelagic fishes in the San Francisco Estuary. These authors considered many hypotheses for declines in abundance, including changes in stock-recruitment relationships and food webs, mortality from predation and water diversions, contaminants, and changes in the physical environment. Multiple-species models with explicit life history submodels could be used to compare the relative likelihood of these alternative hypotheses conditional on the available data. Formal model selection procedures, such as reversible jump MCMC (Green 1995), could be used to estimate posterior probabilities for the models corresponding to different hypotheses.

It is possible, however, that the change-points were caused by variables that have not been measured, or have not been measured long enough to provide data useful in statistical analyses. For example, of the potentially contributing variables listed by Sommer et al. (2007, Fig. 6), only a few could be included in the models. The effects of toxic algae, for example, have only recently been measured and may have increased. Contaminants are too numerous and dispersed, and effects too sporadic and subtle, for any monitoring program to provide useful information for correlative analyses. Thus, these effects must be investigated through more detailed, mechanistic studies.

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Literature cited

Abrahams M., and M. Kattenfeld. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40: 169–174.

Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37: 946-955.

Baskerville-Bridges B., J. C. Lindberg, S. I. Doroshov. 2004. The effect of light intensity, alga concentration, and prey density on the feeding behavior of delta smelt larvae. In: Feyrer F, Brown LR, Brown RL, Orsi JJ, editors. Early life history of fishes in the San Francisco Estuary and watershed. American Fisheries Society Symposium 39. Bethesda (MD): American Fisheries Society. p 219-228.

Baxter, R., R. Breuer, L. Brown, M. Chotkowski, F. Feyrer, M. Gingras, B. Herbold, A. Mueller-Solger, M. Nobriga, T. Sommer, and K. Souza. 2008. Pelagic organism decline progress report: 2007 synthesis of results. Interagency Ecological Program for the San Francisco Estuary, Technical Report 227.

Beal, M. J., Falciani, F., Z. Ghahramani, C. Rangel, and D. L. Wild. 2005. A Bayesian approach to reconstructing genetic regulatory networks with hidden factors. Bioinformatics 21: 349356.

Beckage, B. L. Joseph, P. Belisle, D. B. Wolfson and W. J. Platt. 2007. Bayesian change-point analyses in ecology. New Phytologist 174: 456-467.

Bennett, W. A. 2005. Critical Assessment of the Delta Smelt Population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3: Issue 2 Article 1.

Bennett, W. A. and P. B. Moyle. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin estuary. Pages 519-542 in J. T.

Hollibaugh (ed.), San Francisco Bay: the ecosystem, further investigations into the natural history of San Francisco Bay and Delta with reference to the influence of man. San Francisco. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.

Blaber S. J. M., and T. G. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17: 143–162.

Brower, A., C. Reedy, and J. Yelin-Kefer. 2001. Consensus versus conservation in the upper Colorado River Basin Recovery Implementation Program. Conservation Biology 15: 1001–1007.

Brown, L. R. and P. B. Moyle. 2005. Native fish communities of the Sacramento-San Joaquin watershed, California: a history of decline. Pages 75-98 in F. Rinne, R. Hughes, and R. Calamusso, editors. Fish Communities of Large Rivers of the United States. American Fisheries Society, Bethesda, Maryland.

Carrigan, G., A. G. Barnett, A. J. Dobson, and G. Mishra. 2007. Compensating for missing data from longitudinal studies using WinBUGS. journal of Statistical Software 19:1-17.

Chipman, H., E. George, and R. McCulloch. 2008. BART: Bayesian Additive Regression Trees. Available at http: //www-stat.wharton.upenn.edu/~edgeorge/Research_papers/BART%20June%2008.pdf

Cressie, N., C. A. Calder, J. S. Clark, J. M. V. Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. Ecological Applications 19: 553-570.

Cunningham, S., R. Mac Nally, J. Read, P. Baker, M. White, J. R. Thomson, and P. Griffioen. 2009. A robust technique for mapping vegetation across a major river system. Ecosystems 12: 207-219.

Dege, M. and L. R. Brown. 2004. Springtime Distribution and Abundance of Larval and

Juvenile Fishes in the Upper San Francisco Estuary. Pages 49-66 in F. Feyrer, L.R. Brown, R. Brown, and J. Orsi, editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Bethesda, Maryland.

Denison, D. G. T., B. K. Mallick, and A. F. M. Smith. 1998. Automatic Bayesian Curve Fitting: Journal of the Royal Statistical Society. Series B 60: 333-350.

Dennis, B., M. J. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density dependence, process noise, and observation error. Ecological Monographs76: 323-341.

Fearnhead, P. 2006. Exact and efficient Bayesian inference for multiple changepoint problems. Statistical Computing, 16: 203 - 213.

Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67: 277 - 288.

Feyrer, F., M. L. Nobriga, and T. R. Sommer. 2007. Multi-decadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 64: 723-734.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. Bayesian Analysis 1: 515-533.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian Data Analysis, 2nd Ed., Chapman and Hall, New York, New York.

George, E. I. and D. P. Foster. 2000. Calibration and empirical Bayes variable selection. Biometrika 87: 731-747.

Green, P. 1995. Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. Biometrika 82: 711-732.

Gregory R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127: 275–285.

Harrell, F.E. 2001. Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis, 2nd Ed. Springer, New York.

Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecological Applications 5: 272-289.

Jeffreys, H. 1961. Theory of Probability, 3rd Edition. Clarendon Press, Oxford, England.

Kass, R. and A. Raftery. 1995. Bayes Factors. Journal of the American Statistical Association 90: 773-795.

Kimmerer, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Marine Ecology Progress Series 243: 39-55.

Kimmerer, W.J. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2: , Issue 1 Article 1.

Kimmerer, W. J. 2006. Response of anchovies dampens effects of the invasive bivalve Corbula amurensis on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324: 207-218.

Kimmerer, W. J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 6: Issue 2 Article 2.

Kimmerer, W. J., and J. J. Orsi. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. San Francisco Bay: The Ecosystem, ed. J. T. Hollibaugh, 403-424. San Francisco, AAAS.

Kimmerer, W. J., E. S. Gross, and M. Macwilliams. 2009. Variation of physical habitat for estuarine nekton with freshwater flow in the San Francisco Estuary. Estuaries and Coasts 32: 375-389.

Kimmerer, W. J., J. H. Cowan, Jr., L. W. Miller, and K. A. Rose. 2000. Analysis of an estuarine striped bass population: Influence of density-dependent mortality between metamorphosis and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 57: 478-486.

Kimmerer, W. J., J. H. Cowan, L. W. Miller, and K. A. Rose. 2001. Analysis of an estuarine striped bass population: Effects of environmental conditions during early life. Estuaries 24: 556-574.

Lotze, H.K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312: 1806 – 1809.

Lunn, D. J., A. Thomas, N. Best, and D. Speigelhalter. 2000. WinBUGS -- a Bayesian modeling framework: concepts, structure, and estensibility. Statistics and Computing 10: 325-337.

Lunn, D. J., N. Best, and J. Whittaker. 2008. Generic reversible jump MCMC using graphical models, *Statistics and Computing*, DOI: 10.1007/s11222-008-9100-0

Lunn, D. J., J. C. Whittaker, and N. Best. 2006. A Bayesian toolkit for genetic association studies. Genetic Epidemiology 30: 231-247.

Mac Nally, R., J. R. Thomson, W. J. Kimmerer, F. Feyrer, K. B. Newman, A. Sih, W. A. Bennett, L. Brown, E. Fleishman, S. D. Culberson, and G. Castillo *in press*. An analysis of pelagic species decline in the upper San Francisco Estuary using Multivariate Autoregressive modelling (MAR). Ecological Applications.

Mager R., S. I. Doroshov, J. P. Van Eenennaam, and R. L. Brown. 2004. Early life stages of delta smelt. In: Freyer, F, Brown LR, Brown RL, Orsi JJ, editors. Early life history of fishes in the San Francisco Estuary and watershed. American Fisheries Society Symposium 39. Bethesda, MD: American Fisheries Society. p 169-180.

Manly, B. F. J. 2005a. Analyses A: Log-Linear Modeling, Linear Regression, and Principal Components Analysis for Fall Midwater Trawl Fish Counts, 1967-2004. In B. F. J. Manly and M. Chotkowski. 2005. Progress report on analysis of historical fish and zooplankton population dynamics. Draft report prepared for the Interagency Ecological Program, available at http://science.calwater.ca.gov/pdf/workshops/POD/CDFG_POD_Analysis_of_historical_pelagic_fish_trends.pdf.

Manly, B. F. J. 2005b. Analyses C: Change Point Analyses of the Fall Mid-Water Trawl and the Bay Study Fish Counts. In B. F. J. Manly and M. Chotkowski. 2005. Progress report on analysis of historical fish and zooplankton population dynamics. Draft report prepared for the Interagency Ecological Program, available at http://science.calwater.ca.gov/pdf/workshops/POD/CDFG_POD_Analysis_of_historical_pelagic_fish_trends.pdf.

Manly, B. F. J. and M. Chotkowski. 2006. Two new methods for regime change analysis. Archives fur Hydrobiologia. 167: 593–607.

Moyle, P.B. 2002. Inland Fishes of California, Expanded and Revised. University of California Press, Berkeley.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The Modification of An Estuary. Science 231: 567-573.

Nobriga, M., T. Sommer, F. Feyrer, and K. Fleming. 2008. Long-term trends in summertime habitat suitability for delta smelt, Hypomesus transpacificus. San Francisco Estuary and Watershed Science 6: Issue 1 Article 1.

Orsi, J. J., and W. L. Mecum. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary. San Francisco Bay: The ecosystem, ed. J. T. Hollibaugh, 375-401. San Francisco, AAAS.

Palmer, M.A., C.A.R. Liermann, C. Nilsson, M. Florke, J. Alcamo, P. S. Lake, and N. Bond. 2008. Climate change and the world's river basins: anticipating management options. Frontiers in Ecology and the Environment 6: 81-89.

Quist, M.C., W.A. Hubert, and F.J. Rahel. 2004. Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri River drainage of Wyoming. Transactions of the American Fisheries Society 133: 727–742.

Rosenfield, J. A., and R. D. Baxter. 2007. Population Dynamics and Distribution Patterns of Longfin Smelt in the San Francisco Estuary. Transactions of the American Fisheries Society 136: 1577-1592.

Sala, O., F. Chapin, J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. Huenneke, R. Jackson, A. Kinzig, R. Leemans, D. Lodge, H. Mooney, M. Oesterheld, N. Poff, M. Sykes, B. Walker, M. Walker, and D. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770-74.

Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga, K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries 32: 270-277.

Wanger, O. W. 2007a. Interim remedial order following summary judgment and evidentiary hearing, Case 1: 05-cv-01207-OWW-GSA, Document 560. United States District Court, Eastern District of California, Fresno, California.

Wanger, O. W. 2007b. Findings of fact and conclusions of law re interim remedies re: delta smelt ESA remand and reconsultation, Case 1: 05-cv-01207-OWW-GSA, Document 561. United States District Court, Eastern District of California, Fresno, California.

Webb, J. A. and E. L. King. 2009. A Bayesian hierarchical trend analysis finds strong evidence for large-scale temporal declines in stream ecological condition around Melbourne, Australia. Ecography 32: 215-225.

Table 1 Definitions of variables used in change-point models, years for which data were available, and ranges of values for variables. "Candidate" indicates the species (by number) for which each covariate was included as a candidate predictor in variable selection models. Abbreviated names for covariates used in Figures (3C, 4C, 5C, and 6C) are shown in parentheses. The data, along with further details and explanations, are available at http://knb.ecoinformatics.org/knb/metacat/nceas.958.8/nceas/. See also Mac Nally et al (in review) Table 2.

Variable	Years (missing)	Range	Candidate	Definition
Response variables				
Delta smelt (*Hypomesus transpacificus*)[1]	1967–2007 (3)	0.06–4.02		Autumn (September–December) midwater trawl, average total catch per trawl
Longfin smelt (*Spirinchus thaleichthys*)[2]	1967–2007 (3)	0.03–113.16		Autumn (September–December) midwater trawl, average total catch per trawl
Striped bass (*Morone saxatilis*)[3]	1967–2007 (3)	0.12–59.38		Autumn (September–December) midwater trawl, average age-0 catch per trawl
Threadfin shad (*Dorosoma petenense*)[4]	1967–2007 (3)	1.36–31.21		Autumn (September–December) midwater trawl, average total catch per trawl

Covariates				
Calanoid copepods – spring (cal.sp)	1972–2007 (1)	0.98–43.87	all	Average biomass (mg C m^{-3}) of calanoid copepodites and adults during spring (March-May) in low-salinity zone (0.5–10 ‰)
Calanoid copepods – summer (cal.s)	1972–2007 (1)	2.93–27.62	all	Average biomass (mg C m^{-3}) of calanoid copepodites and adults during summer (June-September) in low-salinity zone (0.5–10 ‰)
Mysids	1972–2007 (0)	0.42–35.05	2,3	Average biomass of mysid shrimp (mg C m^{-3}) in low salinity zone during June-September in low-salinity zone (0.5–10 ‰)
Northern anchovy (*Engraulis mordax*) (Anchovy)	1980–2006 (1)	0.22–490.42	1,2,3	Average catch per trawl of northern anchovy in the Bay Study midwater trawl (June-September) in the low salinity zone (0.5-10 ‰)
“Other zooplankton” in spring (zoop)	1972–2006 (0)	3.79–56.86	4	Average biomass (mg C m^{-3}) of other zooplankton (not including crab and barnacle larvae, cumaceans) during spring (March-May) in the freshwater zone (< 0.5 ‰)
Spring chlorophyll *a* (low salinity zone)	1975–2006 (0)	1.12–21.32	all	Average mg chl *a* m^{-3} during spring (March-May) in low

(chlo.sp)				salinity zone (0.5-10 ‰)
Cyclopoid copepod *Limnoithona tetraspina* (Limno.)	1972–2006 (0)	0–7.78	1,2,4	Average biomass (mg C m^{-3}) of *Limnoithona* copepodites and adults during summer (June-September) in the low salinity zone (0.5-10 ‰)
Inland silverside (*Menidia beryllina*) (silver.)	1994–2006 (0)	19.88–116.54	all	Average catch per seine haul of inland silverside in the U.S. Fish and Wildlife Service survey during July-September (for stations within the delta)
Largemouth bass (*Micropterus salmoides*) (lm_bass)	1994–2006 (0)	0.02–8.00	all	Average catch per seine haul of largemouth bass in the U.S. Fish and Wildlife Service survey during July-September (for stations within the delta)
Spring X2 (isohaline) (X2.sp)	1967–2006 (0)	48.53–91.74	1,2,3	Average March-May position of the 2 ‰ isohaline (X2) measured in km upstream from the Golden Gate Bridge
Autumn X2 (isohaline) (X2.aut)	1967–2006 (0)	60.24–93.18	4	Average during September-December position of the 2 ‰ isohaline (X2) measured in km upstream from the Golden Gate Bridge
Water clarity (clarity)	1967–2006 (0)	0.44 – 11.00	all	Average Secchi depth (m) for the autumn midwater trawl

				survey
Winter exports (expt.w)	1967–2006 (0)	0.13–12.00	1,2,4	Total volume of water (km^3) exported by the California State Water Project and Central Valley Project during December-February.
Spring exports (expt.s)	1967–2006 (0)	0.37–13.00	all	Total volume of water (km^3) exported by the California State Water Project and Central Valley Project during March-May.
Duration of spawning window for delta smelt (15-20C)	1975–2007 (0)	24 – 85	1	Number of days for which average temperature was between 15-20 °C [range of water temperatures that best induce spawning by delta smelt (15 °C) and limit larval survivorship (20 °C)], mean of 5 continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta
Average summer water temperature (temp)	1967–2006 (0)	20.45 – 23.65	all	Average water temperature (°C), mean of 5 continuous stations monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta during June-September
Winter Pacific Decadal Oscillation	1967–2007 (0)	-1.90 – 1.89	2,3	December-February

(PDO.w)				
Summer Pacific Decadal Oscillation (PDO.s)	1967–2007 (0)	-1.11 – 2.52	1,2,3	June-September
Striped bass egg supply (eggs)	1970-2006 (0)	0.02 – 0.40	3	Estimated striped bass egg supply, calculated as the sum of age-specific fecundity based on the population estimates generated by the California Department of Fish and Game Kimmerer et al. (2000)

Table 2. Summary of covariate effects in models of annual abundance of four species of pelagic fishes in the San Francisco Estuary. We used a variable selection model (5) to select covariates and included the covariates in subsequent models if their posterior probability of inclusion (***Pr.*** in table 2) exceeded 0.75* (see Figures 4, 6, 8, 10 for corresponding values for all variables). Mean slope is the posterior mean of the average linear slope over the full range of covariate values in a piecewise linear spline model with up to 3 knots (changes in slope). All fitted splines were monotonic, and departures from linearity generally were moderate and are described in the "functional response" column. If the estimated functional response varied between single species[1] and multispecies[2] models both are described in "functional response." Estimated covariate effects are conditional on the variable being a predictor, but incorporate uncertainties about the number and timing of change-points. R^2 shows the relative fits of the posterior medians of the fitted values (n_ts in equation 6) to the observed log abundance data. Corresponding R^2 values for trend models were delta smelt, 0.74; longfin smelt, 0.69; striped bass, 0.85; threadfin shad, 0.69.

		Single species model[1]			**Multispecies model[2]**			
	Pr.	**Mean (SD)**	**95% CI**	***R*²**	**Mean (SD)**	**95% CI**	***R*²**	**Functional response**
Delta smelt				.65			.63	
water clarity	0.81	-0.24 (0.29)	(-0.85, 0.29)		-0.24 (0.26)	(-0.74, 0.30)		1: weak at values >2 SD from mean 2: stronger at values > 1 SD
winter exports	0.77	-0.25 (0.18)	(-0.60, 0.09)		-0.22 (0.17)	(-0.55, 0.11)		weaker at values < -1 SD
Longfin smelt				.88			.85	

spring X2	1.00	-1.25 (0.18)	(-1.61, -0.88)		-1.20 (0.18)	(-1.55, -0.83)		stronger at values > mean
water clarity	0.96	-0.15 (0.43)	(-1.05, 0.58)		-0.27 (0.41)	(-1.14, 0.48)		stronger at values > 1 SD
Striped bass				.88			.89	
water clarity	0.99	-0.59 (0.24)	(-1.04, -0.06)		-0.57 (0.27)	(-1.06, -0.03)		linear
ρ	0.98	0.38 (0.17)	(0.05, 0.69)		0.40 (0.13)	(0.11, 0.66)		
Threadfin shad				.45			.46	
winter exports	0.51*	-0.14 (0.19)	(-0.52, 0.25)		-0.10 (0.18)	(-0.45, 0.28)		1 weak at values < mean 2 linear
spring exports	0.59*	-0.22 (0.14)	(-0.50, 0.06)		-0.23 (0.14)	(-0.48, 0.03)		1 weaker at values < -1.5 SD 2 linear

*Winter and spring exports were included in models for threadfin shad because probabilities of inclusion were sensitive to prior distributions on linear coefficients. Probabilities exceeded 0.75 under certain, more restrictive prior distributions (see main text and Appendix A)

Figure legends

Fig. 1. Location and physiography of the upper San Francisco Estuary, California, USA. • denote sampling locations of the autumn midwater trawl surveys; arrows indicate two representative positions of the 2 ‰ isohaline (X2); SWP (State Water Project) and CVP (Central Valley Project) are locations of water exports from the estuary.

Fig. 2. Examples of change-point models. All examples show a hypothetical time series ***y*** (dots) and corresponding piecewise linear models (dark lines). A: step change at time 31, modeled by $y_t = 2 - 0.75I(t \geq 31) - 0.02t + \varepsilon_t$. B: step change at time 21 and trend change at time 31, modeled by $y_t = 2 - 1I(t \geq 21) - 0.03(t-31)I(t \geq 31) + \varepsilon_t$. C: covariate model with step change at time 31, modeled by $y_t = 0 - 0.75I(t \geq 31) + 0.5x_t + \varepsilon_t$. D: covariate model with no change-points (change-point at time 31 in C is predicted by covariate), modeled by $y_t = 0 + 0.5x_t + \varepsilon_t$. In C and D, grey lines show the time series of the covariate x.

Fig. 3. A: Results of trend model (equation 2) for delta smelt. Fitted trend is shown as a black line and observed values (mean log catch per autumn trawl ± SE) as points. Intercept (α_t) values are shown as a dashed grey line, and the trend component ($f_t(t)$) as a solid grey line. Bottom panel shows posterior probabilities of step changes (black) or trend changes (grey) in each year for the trend model (equation 2). B: Results of covariate-conditioned change-point model (eq. 6) for delta smelt. Fitted values are shown as a black line, the intercept (α_t) as a dashed grey line, and the covariate component (*f*(water clarity) + *f*(winter exports), where *f*() is a linear spline) as a solid grey line. The posterior probabilities of step changes (abrupt changes unexplained by covariates) for each year are shown in the bottom panel. C: Results of covariate selection model (eq. 5) for delta smelt. Posterior probabilities of variable inclusion (grey bars, right axis) and posterior mean (± 1 SE) linear coefficients (black bars, left axis) are shown for each candidate predictor. Refer to table 1 for explanation of covariates. Mean linear

coefficients were calculated as the mean slope of the fitted linear-spline model over the data range. In A, B, and C horizontal dashed lines show posterior probabilities corresponding to odds ratios of 3 (= 0.14 for change-points, = 0.75 for variable inclusion), which we consider substantial evidence for a change-point occurring in a year (A and B) or for a variable having an effect on abundance (C). In C the prior probability of inclusion (0.5) is shown as a dotted line.

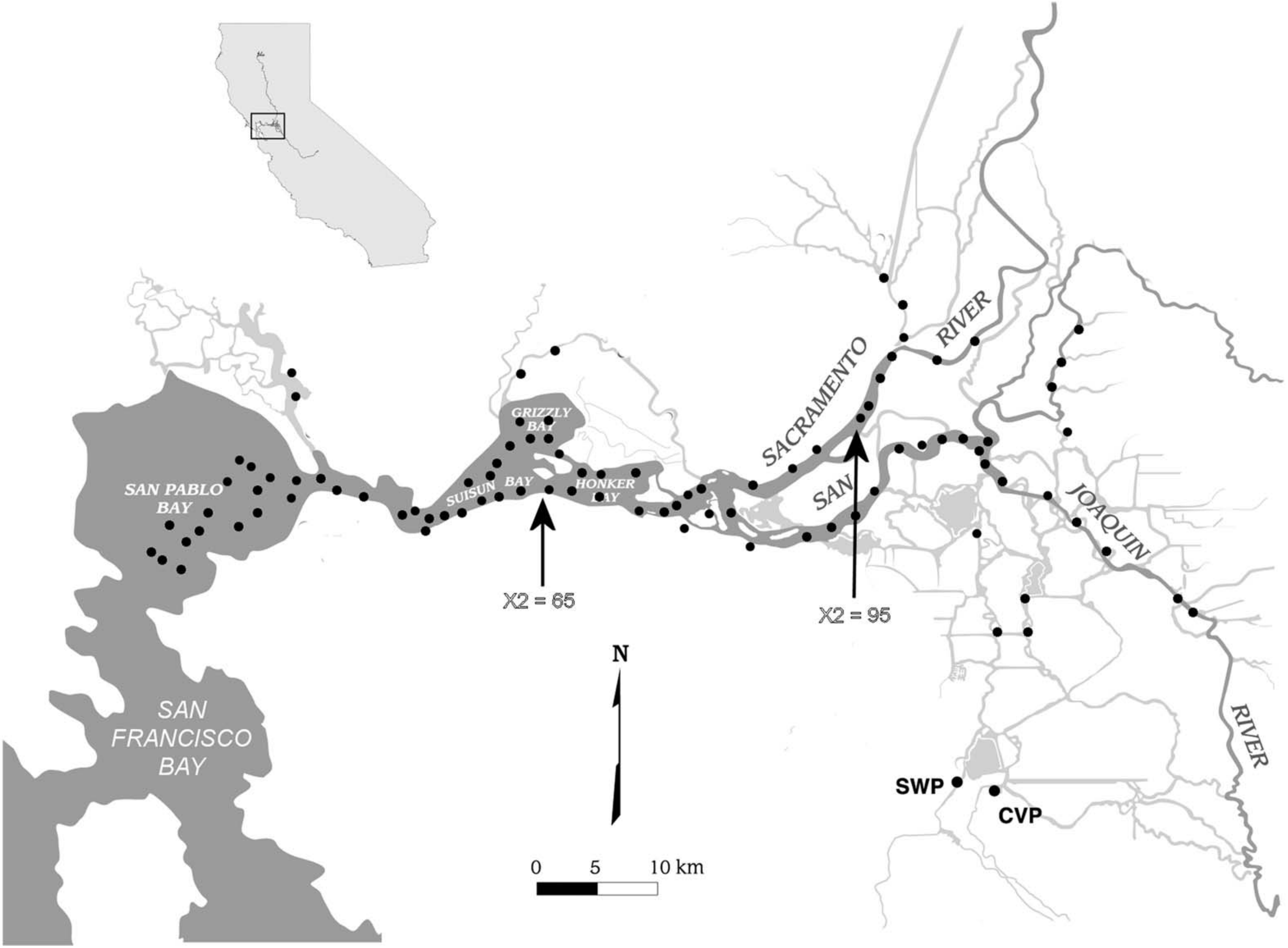
Fig. 4. Striped bass. Plot format as in Fig. 3. In B, the covariate component (solid grey line) represents *f*(water clarity) + ρn_{t-1}. The grey bars in B show the posterior probabilities of change-points in each year if $\rho = 0$.

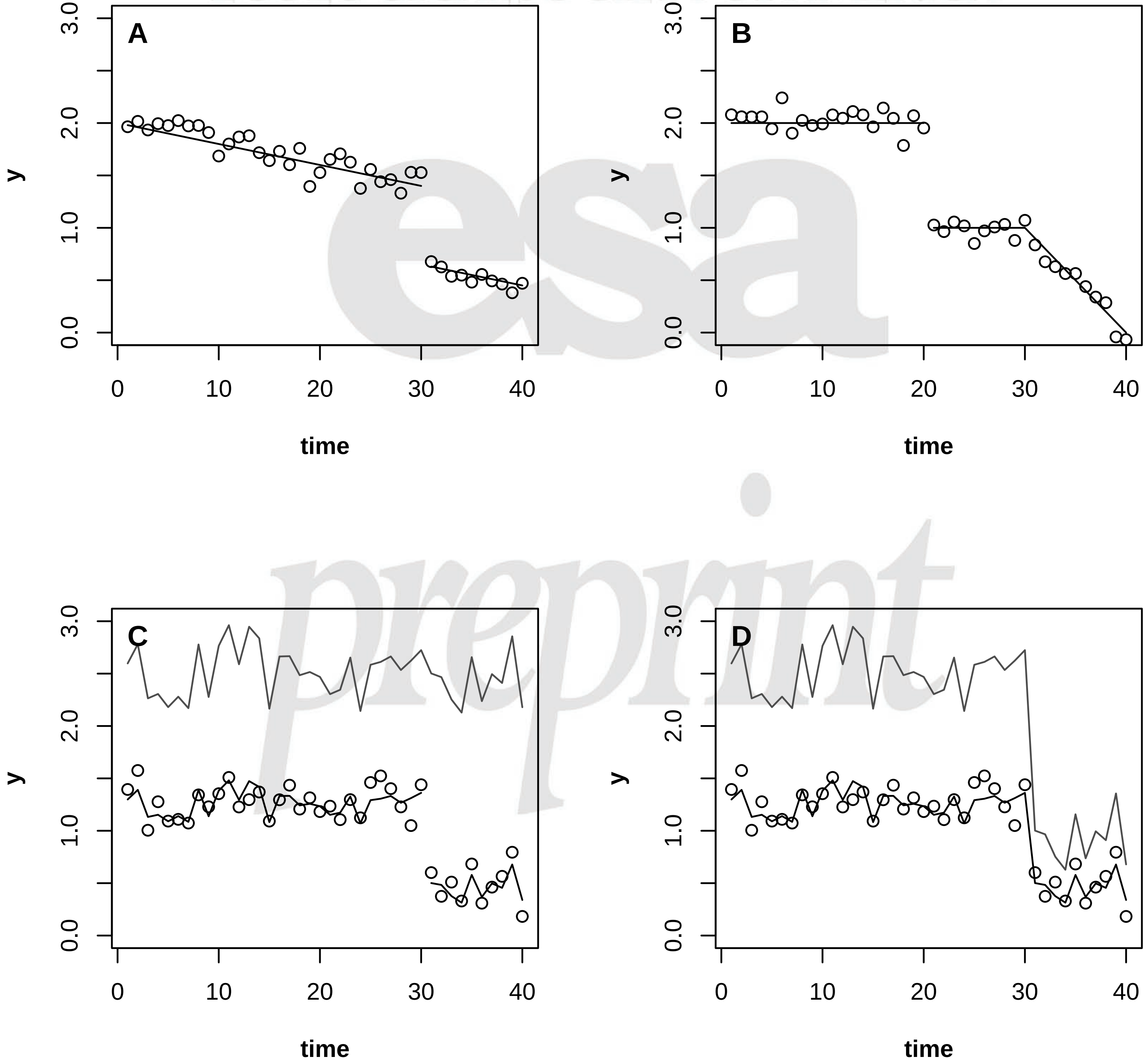
Fig. 5. Threadfin shad. Plot format as in Fig. 3. In B, the covariate component (solid grey line) represents *f*(winter exports) + *f*(spring exports) and the dashed grey line represents the time-dependent intercept α_t plus a non-linear trend *f*(*t*).

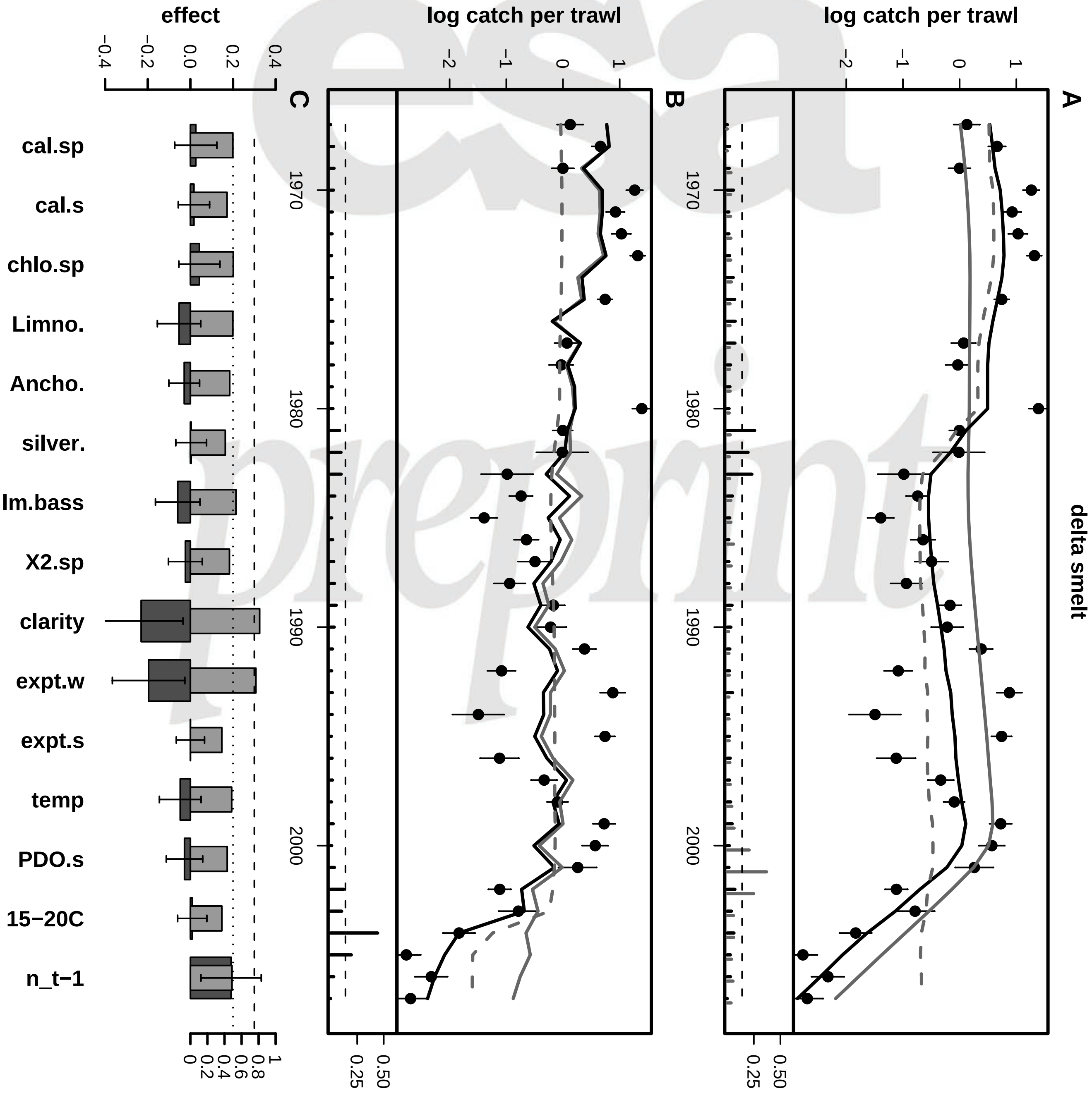
Fig. 6. Longfin smelt. Plot format as in Fig. 3. In B, the covariate component (solid grey line) represents *f*(water clarity) + *f*(spring X2), but *f*(water clarity) was near zero, and including only *f*(spring X2) results in essentially the same figure as this 6B. .

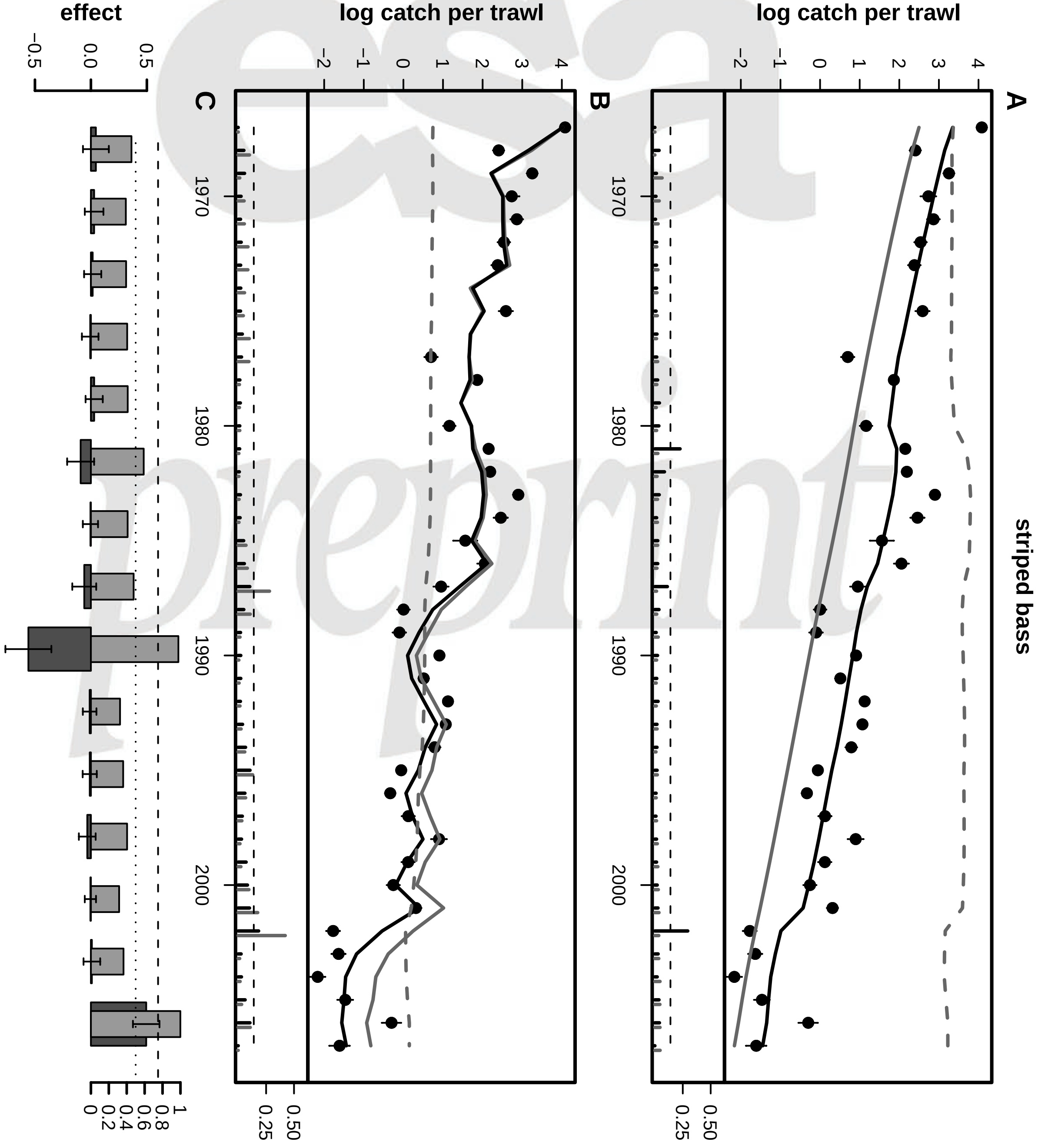
Fig. 7. Abundance (log catch per trawl) with fitted values (solid lines, dashed lines are 95% credible intervals) and intercept parameters (grey solid) for delta smelt, longfin smelt, striped bass, and threadfin shad in the multi-species change-point model. Intercept parameter = species specific intercept plus common change-point parameter. Bars show posterior probabilities (right axis) of common (black) and species-specific (grey) change-points in each year.

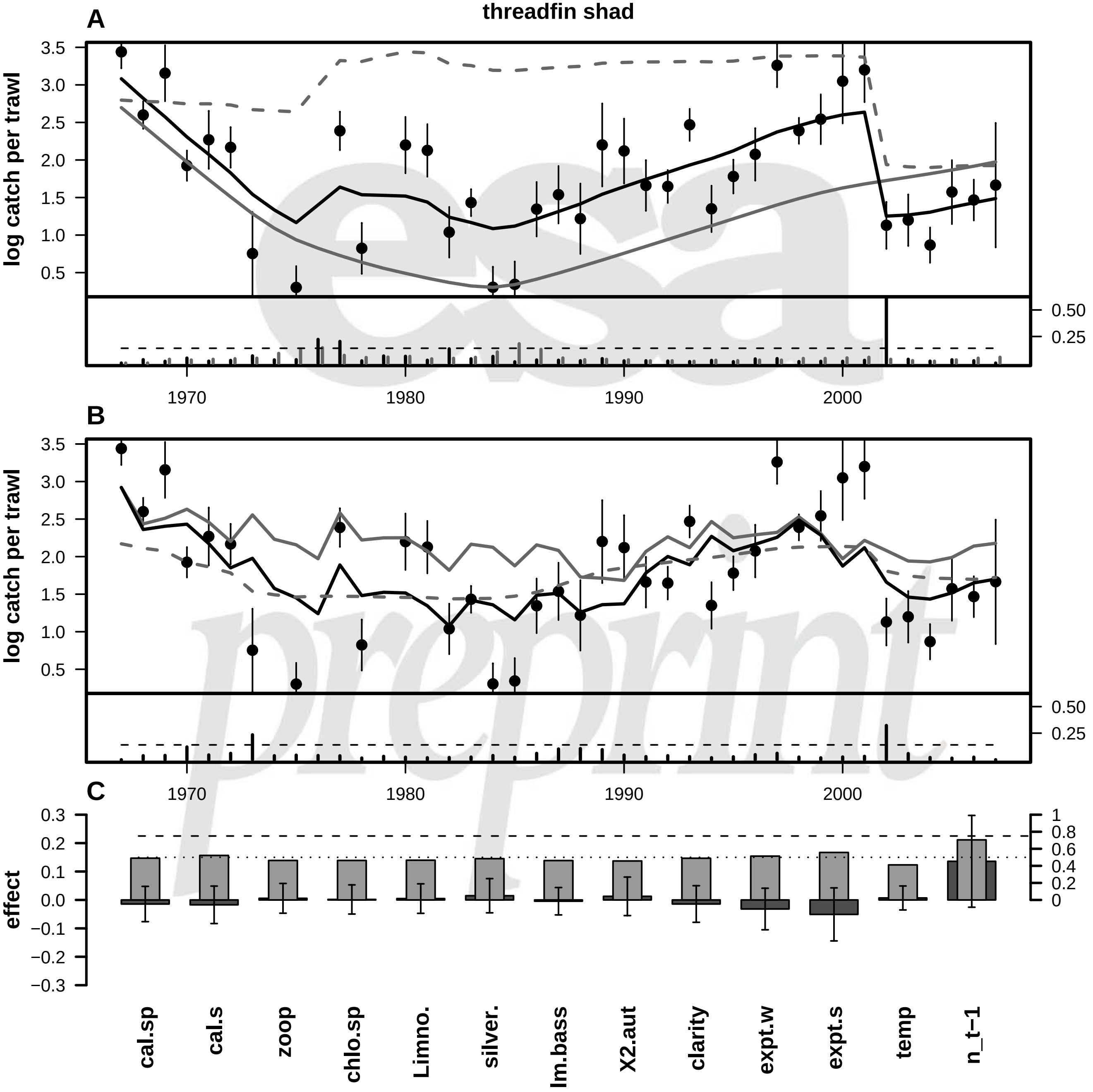
Fig. 8. Trends in covariates used in covariate-conditioned change-point models.

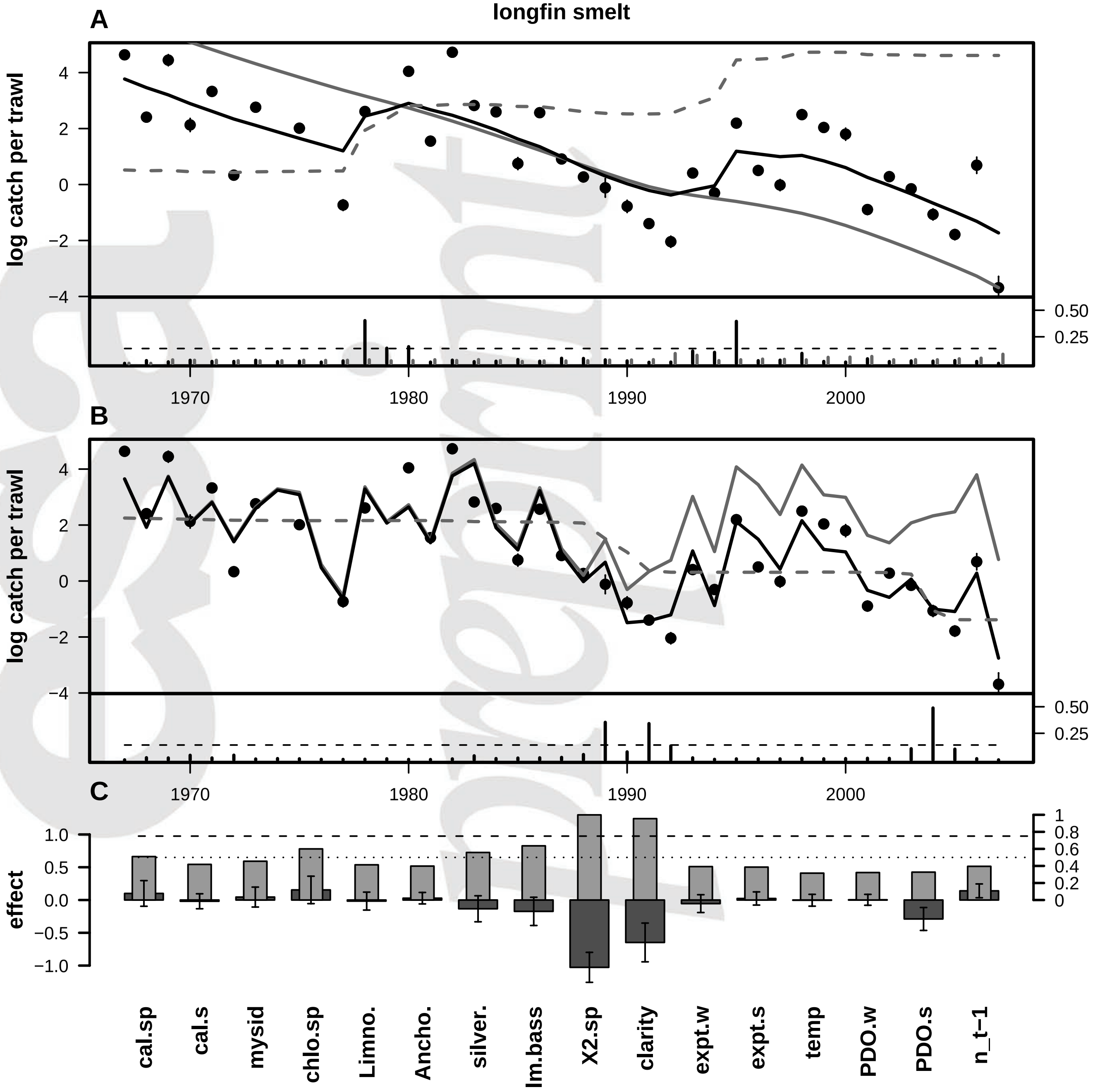

SAN PABLO BAY
SAN FRANCISCO BAY
GRIZZLY BAY
SUISUN BAY
HONKER BAY
SACRAMENTO RIVER
SAN JOAQUIN RIVER
X2 = 65
X2 = 95
N
0
5
10 km
SWP
CVP

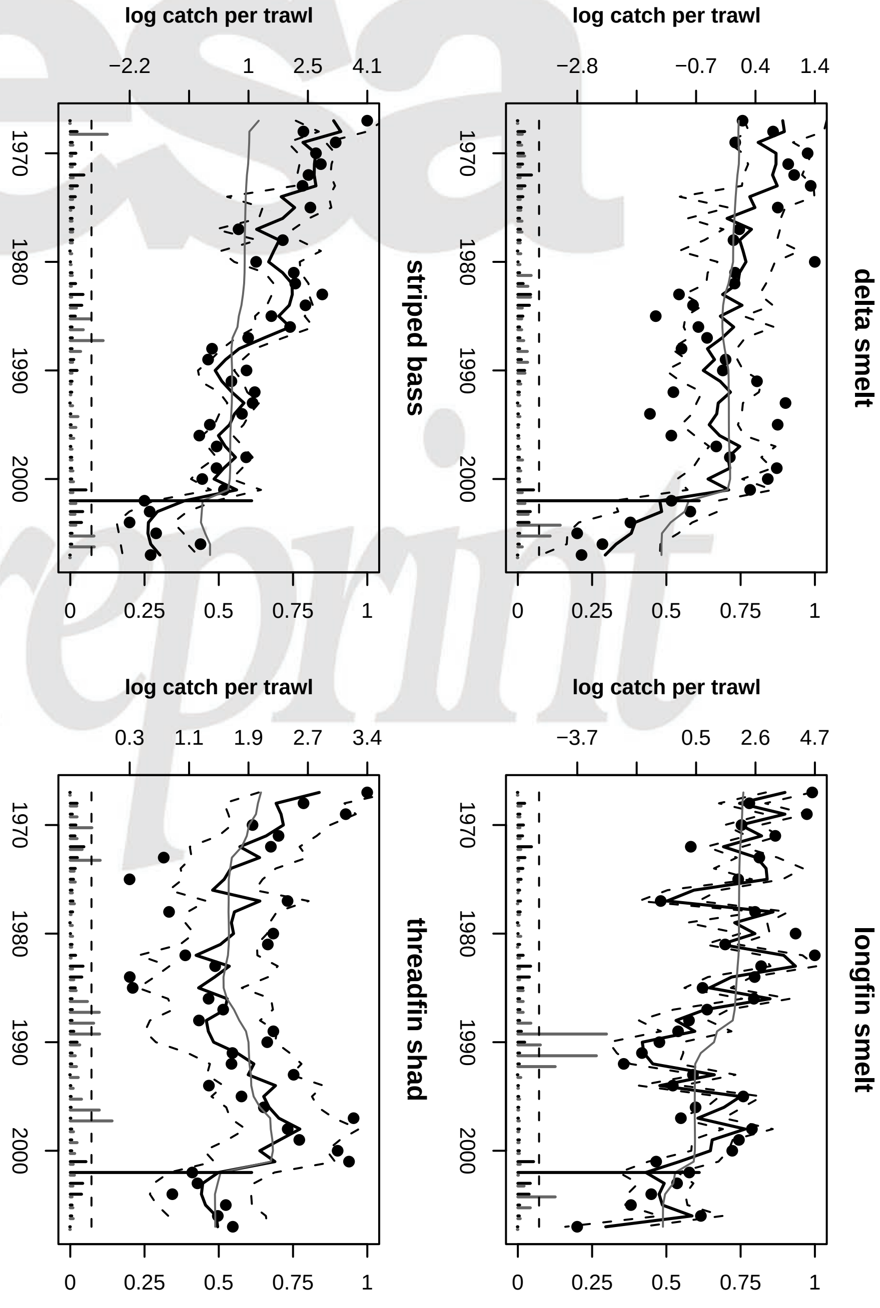

A
B
C
D
y
time
0.0
1.0
2.0
3.0
0
10
20
30
40

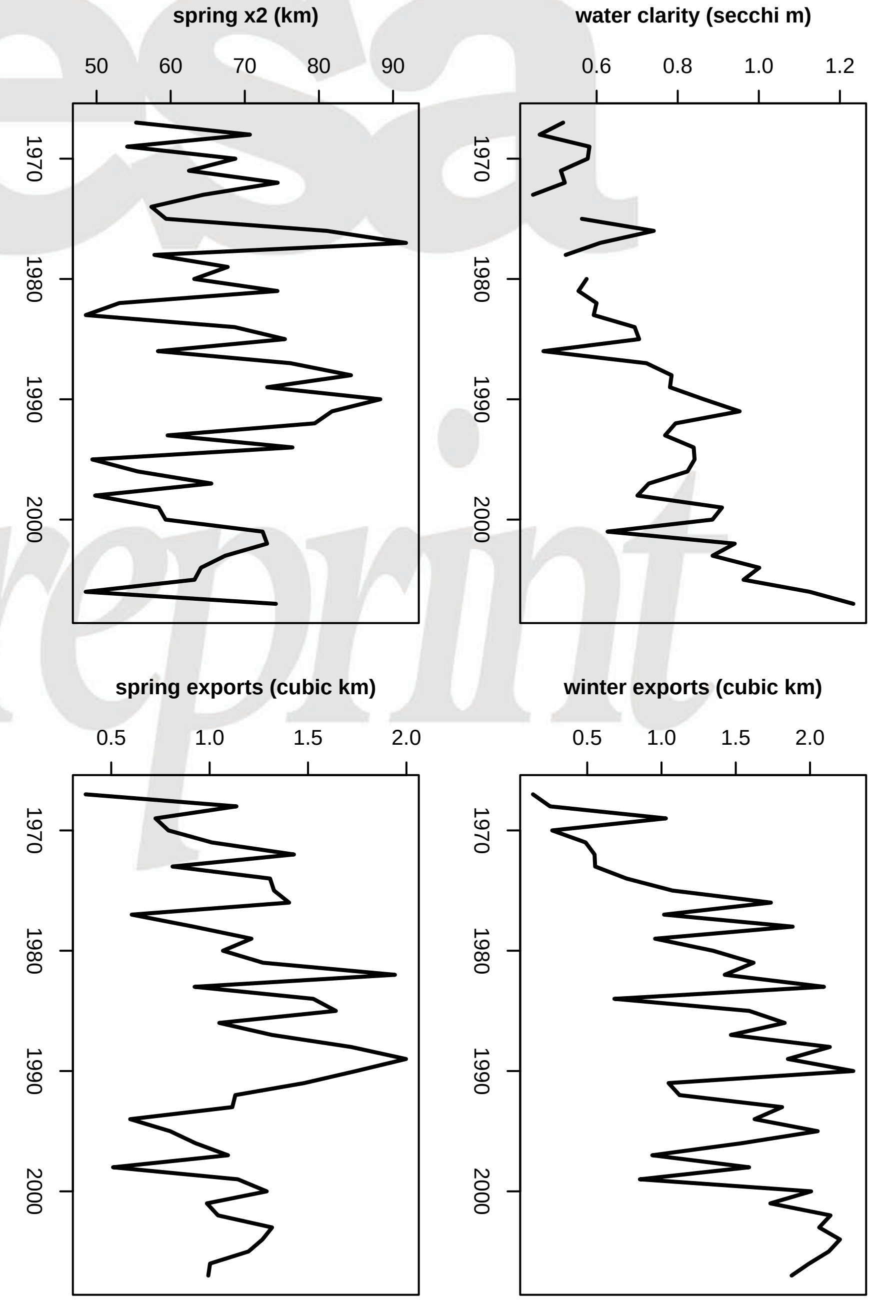

A
B
C
delta smelt
log catch per trawl
log catch per trawl
−2
−1
0
1
1970
1980
1990
2000
0.25
0.50
effect
−0.4
−0.2
0.0
0.2
0.4
cal.sp
cal.s
chlo.sp
Limno.
Ancho.
silver.
lm.bass
X2.sp
clarity
expt.w
expt.s
temp
PDO.s
15−20C
n_t−1
0
0.2
0.4
0.6
0.8
1


A
striped bass
log catch per trawl
−2
−1
0
1
2
3
4
1970
1980
1990
2000
0.25
0.50
B
log catch per trawl
C
effect
−0.5
0.0
0.5
cal.sp
cal.s
mysid
chlo.sp
Ancho.
silver.
lm.bass
X2.sp
clarity
expt.s
temp
PDO.w
PDO.s
eggs
n_t−1
0
0.2
0.4
0.6
0.8
1


threadfin shad
A
B
C
log catch per trawl
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.50
0.25
1970
1980
1990
2000
effect
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
1
0.8
0.6
0.4
0.2
0
cal.sp
cal.s
zoop
chlo.sp
Limno.
silver.
lm.bass
X2.aut
clarity
expt.w
expt.s
temp
n_t−1


longfin smelt
A
log catch per trawl
4
2
0
−2
−4
0.50
0.25
1970
1980
1990
2000
B
log catch per trawl
4
2
0
−2
−4
0.50
0.25
1970
1980
1990
2000
C
effect
1.0
0.5
0.0
−0.5
−1.0
1
0.8
0.6
0.4
0.2
0
cal.sp
cal.s
mysid
chlo.sp
Limno.
Ancho.
silver.
lm.bass
X2.sp
clarity
expt.w
expt.s
temp
PDO.w
PDO.s
n_t−1


striped bass
delta smelt
threadfin shad
longfin smelt
log catch per trawl
−2.2
1
2.5
4.1
−2.8
−0.7
0.4
1.4
0.3
1.1
1.9
2.7
3.4
−3.7
0.5
2.6
4.7
1970
1980
1990
2000
0
0.25
0.5
0.75
1


spring x2 (km)
50
60
70
80
90
1970
1980
1990
2000
water clarity (secchi m)
0.6
0.8
1.0
1.2
1970
1980
1990
2000
spring exports (cubic km)
0.5
1.0
1.5
2.0
1970
1980
1990
2000
winter exports (cubic km)
0.5
1.0
1.5
2.0
1970
1980
1990
2000