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

James R. Thomson,[1,8] Wim J. Kimmerer,[2] Larry R. Brown,[3] Ken B. Newman,[4] Ralph Mac Nally,[1] William A. Bennett,[5] Frederick Feyrer,[6] and Erica Fleishman[7,9]

[1]*Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Melbourne 3800 Australia*
[2]*Romburg Tiburon Center, San Francisco State University, 3152 Paradise Drive, Tiburon, California 94920 USA*
[3]*U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, California 95819-6129 USA*
[4]*U.S. Fish and Wildlife Service, 4001 N. Wilson Way, Stockton, California 95632 USA*
[5]*Center for Watershed Sciences and Bodega Marine Laboratory, University of California, Davis, P.O. Box 247, Bodega Bay, California 94923 USA*
[6]*Applied Science Branch, U.S. Bureau of Reclamation, 2800 Cottage Way, Sacramento, California 95825-1898 USA*
[7]*National Center for Ecological Analysis and Synthesis, University of California, 735 State Street, Suite 300, Santa Barbara, California 93101 USA*

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 refitted change point models conditional on the selected covariates to explore whether those covariates could explain statistical trends or change points in species abundances. We also fitted a multispecies 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‰ 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.

Key words: change point; delta smelt; hierarchical Bayes; longfin smelt; Sacramento–San Joaquin Delta, California, USA; striped bass; threadfin shad; upper San Francisco Estuary, California, USA.

Introduction

Declines in ecological condition across large areas are increasingly common around the world (e.g., Sala et al. 2000, 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 nonnative species (Lotze et al. 2006). The San Francisco Estuary, California, USA, 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 (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 ~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

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[8] E-mail: jim.thomson@sci.monash.edu.au
[9] Present address: Bren School of Environmental Science and Management, 2400 Bren Hall, University of California, Santa Barbara, California 93106-5131 USA.

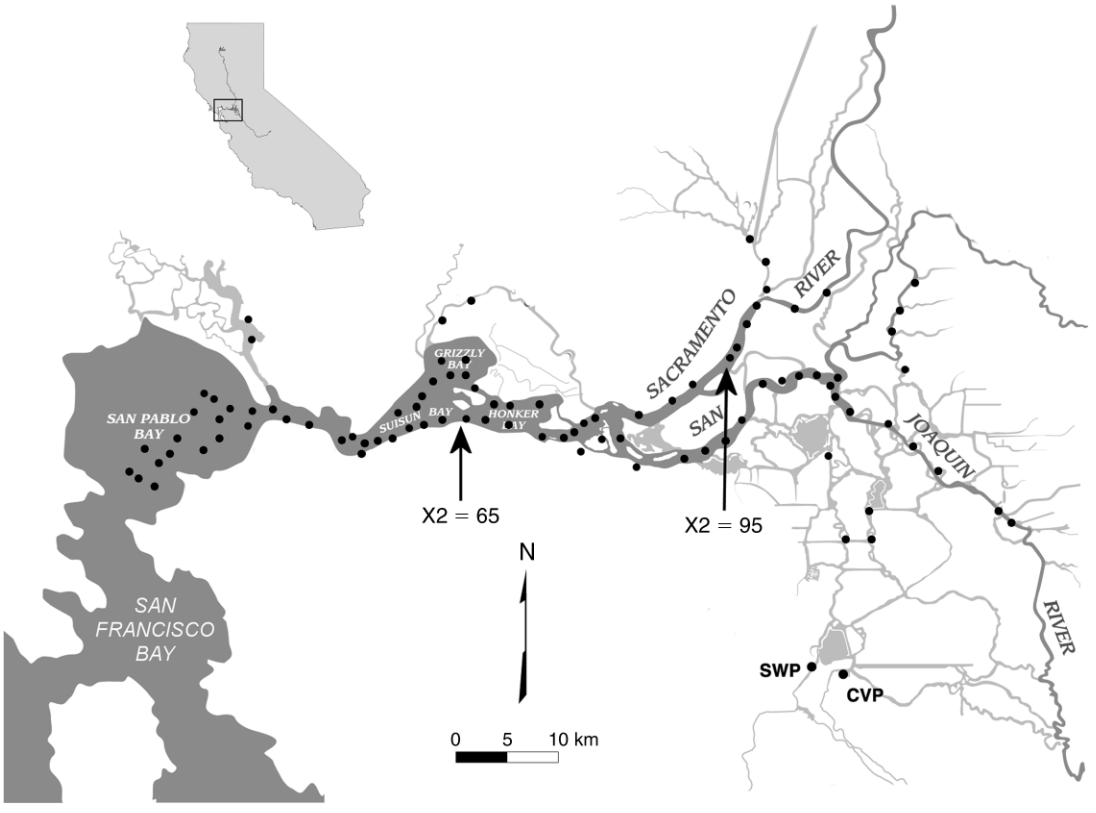

FIG. 1. Location and physiography of the upper San Francisco Estuary, California, USA. Solid circles denote sampling locations of the autumn midwater trawl surveys; arrows indicate two representative positions of the 2‰ isohaline (X2); SWP (State Water Project) and CVP (Central Valley Project) are locations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

production of fruits and vegetables in the United States, frequently approaches US$15 billion. Regulations on water diversions, including standards for the position of the 2‰ 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 ca. 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 2007*a*, *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, 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 toward 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. Manly and Chotkowski (2006) used a bootstrap approach to explore the timing of one or more change

points in the abundance of delta smelt. But 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 (1967–2007), 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 multispecies change point model. Hierarchical Bayesian models are ideally suited to the complexity of analyzing 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 12–15 months after birth. A small percentage live two 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 the 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 were deliberately introduced to the Delta from the east coast of the United States in 1879 and now support a popular sport fishery (Moyle 2002). The 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, Fearnhead 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 multispecies 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 ~400 observations (data and station details *available online*)[10]. We assumed that the observations were unbiased estimates of the true

[10] ⟨http://knb.ecoinformatics.org/knb/metacat/nceas.958.8/nceas/⟩←

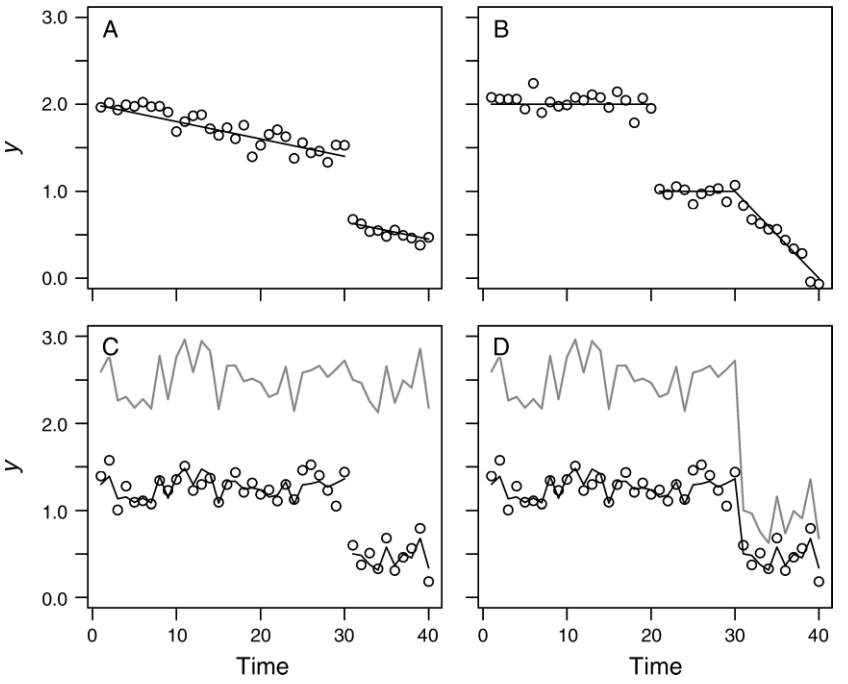

FIG. 2. Examples of change point models. All examples show a hypothetical time series y (circles) and corresponding piecewise linear models (dark lines): (A) a step change at time 31, modeled by $y_t = 2 - 0.75I(t \geq 31) - 0.02t + \varepsilon_t$; (B) a step change at time 21 and trend change at time 31, modeled by $y_t = 2 - 1I(t \geq 21) - 0.03(t - 31)I(t \geq 31) + \varepsilon_t$; (C) a covariate model with step change at time 31, modeled by $y_t = 0 - 0.75I(t \geq 31) + 0.5x_t + \varepsilon_t$; (D) a covariate model with no change points (change point at time 31 in panel C is predicted by covariate), modeled by $y_t = 0 + 0.5x_t + \varepsilon_t$. In panels (C) and (D), gray lines show the time series of the covariate x. For all models, ε_t is the residual error, and all other parameters are as defined in Eqs. 1–3.

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

$$y_t \sim \text{Normal}\left(n_t, \sigma_{\text{O}t}^2\right) \quad (1)$$

$$n_t \sim \text{Lognormal}\left(\alpha_t + f_t(t), \sigma_{\text{p}}^2\right). \quad (2)$$

Simultaneously estimating observation noise, $\sigma_{\text{O}t}$, 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 $\sigma_{\text{O}t}$ in the fitting procedure.

The parameters of the state process model, α_t and $f_t(t)$ in Eq. 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:

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

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 jth 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 (Eq. 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):

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

The term $(t - \theta_j)_+$ equals $I(t \geq \theta_j)(t - \theta_j)$. 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 here. 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: $k \sim$ 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 the Appendix for further discussion of priors). The priors were uninformative with respect to the timing of change points, with equal prior probability [$p_0 = (0.5 \times 4)/39 = 0.05$] of change points in each year (Appendix). 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). 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 (12–15) 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 Eq. 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 nonlinear 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

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

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 nonlinear 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 nonlinear 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

TABLE 1. Definitions of variables used in change point models, years for which data were available, and ranges of values for variables.

Variable	Years (missing)	Range
Response variables		
Delta smelt (*Hypomesus transpacificus*) 1	1967–2007 (3)	0.06–4.02
Longfin smelt (*Spirinchus thaleichthys*) 2	1967–2007 (3)	0.03–113.16
Striped bass (*Morone saxatilis*) 3	1967–2007 (3)	0.12–59.38
Threadfin shad (*Dorosoma petenense*) 4	1967–2007 (3)	1.36–31.21
Covariates		
Calanoid copepods, spring (cal.sp)	1972–2007 (1)	0.98–43.87
Calanoid copepods, summer (cal.s)	1972–2007 (1)	2.93–27.62
Mysids (mysid)	1972–2007 (0)	0.42–35.05
Northern anchovy (*Engraulis mordax*) (Ancho.)	1980–2006 (1)	0.22–490.42
"Other zooplankton," spring (zoop)	1972–2006 (0)	3.79–56.86
Spring chlorophyll *a* in low-salinity zone (chlo.sp)	1975–2006 (0)	1.12–21.32
Cyclopoid copepod *Limnoithona tetraspina* (Limno.)	1972–2006 (0)	0–7.78
Inland silverside (*Menidia beryllina*) (silver.)	1994–2006 (0)	19.88–116.54
Largemouth bass (*Micropterus salmoides*) (lm.bass)	1994–2006 (0)	0.02–8.00
Spring X2 (X2.sp)	1967–2006 (0)	48.53–91.74
Autumn X2 (X2.aut)	1967–2006 (0)	60.24–93.18
Water clarity (clarity)	1967–2006 (0)	0.44–11.00
Winter exports (expt.w)	1967–2006 (0)	0.13–12.00
Spring exports (expt.s)	1967–2006 (0)	0.37–13.00
Duration of spawning window for delta smelt (15-20C)	1975–2007 (0)	24–85
Mean summer water temperature (temp)	1967–2006 (0)	20.45–23.65
Winter Pacific Decadal Oscillation (PDO.w)	1967–2007 (0)	−1.90–1.89
Summer Pacific Decadal Oscillation (PDO.s)	1967–2007 (0)	−1.11–2.52
Striped bass egg supply (eggs)	1970–2006 (0)	0.02–0.40

Notes: "Candidate" indicates the species (by number; see numbers following species) for which each covariate was included as a candidate predictor in variable selection models. Abbreviated names for covariates used in Figs. 3C, 4C, 5C, and 6C are shown in parentheses. Biomass was measured as mg C/m^3. The low-salinity zone was determined to be at 0.5–10‰. The X2 position was measured in km upstream from the Golden Gate Bridge. The data, along with further details and explanations, are *available online* (see footnote 10). See also Mac Nally et al. (2010: Table 2).

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 nonzero covariate effects, scaled so that ~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). Any variables for which $\Pr(k_j > 0)$ values were sensitive to priors are identified in *Results*.

We fitted the variable selection model (Eq. 5) with and without the autocorrelation term ρn_{t-1} and with a conditional prior on $\rho[\rho \,|\, k_{Q+1} = 1 \sim \text{Normal}(0, \sigma_\beta^2);$ $k_{Q+1} \sim \text{Bernoulli}(0.5)]$ 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

TABLE 1. Extended.

Candidate	Definition
	autumn (Sep–Dec) midwater trawl, mean total catch (no. individuals) per trawl
	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
	autumn (Sep–Dec) midwater trawl, mean age-0 catch per trawl
	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
all	mean biomass of calanoid copepodites and adults during spring (Mar–May) in low-salinity zone
all	mean biomass of calanoid copepodites and adults during summer (Jun–Sep) in low-salinity zone
2, 3	mean biomass of mysid shrimp during Jun–Sep in low-salinity zone
1, 2, 3	mean catch per trawl of northern anchovy in the Bay Study midwater trawl (Jun–Sep) in low-salinity zone
4	mean biomass of other zooplankton (not including crab and barnacle larvae, cumaceans) during spring (Mar–May) in the freshwater zone (<0.5‰)
all	mean chl *a* (mg/m^3) during spring (Mar–May) in low-salinity zone
1, 2, 4	mean biomass of *Limnoithona* copepodites and adults during summer (Jun–Sep) in the low-salinity zone
all	mean catch per seine haul of inland silverside in the USFWS survey during Jul–Sep (for stations within the delta)
all	mean catch per seine haul of largemouth bass in the USFWS survey during Jul–Sep (for stations within the delta)
1, 2, 3	mean Mar–May position of the 2‰ isohaline (X2)
4	mean during Sep–Dec position of the 2‰ isohaline (X2)
all	mean Secchi depth (m) for the autumn midwater trawl survey
1, 2, 4	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Dec–Feb
all	total volume of water (km^3) exported by the California State Water Project and Central Valley Project during Mar–May
1	no. days for which mean temperature was between 15° and 20°C (range of water temperatures that best induce spawning by delta smelt [15°C] and limit larval survivorship [20°C]), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta
all	mean water temperature (°C), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta during Jun–Sep
2, 3	Dec–Feb
1, 2, 3	Jun–Sep
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)

covariate-conditioned change point model with $q < Q$ covariates was

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

In this model, k_j had minimum value = 1 and a prior distribution given by $k_j = 1 + \kappa_j$, where $\kappa_j \sim$ 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 nonzero (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 Eq. 6).

In Eq. 6, the covariate effects,

$$\sum_{j=1}^{q}\sum_{m=1}^{k_j}\beta_{jm}(x_{jt} - \phi_{jm})$$

replace the trend component $f_t(t)$ in Eq. 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).

Multispecies model

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

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

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

The multispecies 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 version 1.4 (Lunn et al. 2000) with three chains of 200 000 iterations each after 50 000 iteration burn-in periods. The 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 the Supplement.

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. 4B) and threadfin shad (Fig. 5B) in 2002.

In the multispecies change point models, there was strong evidence of a common change point in 2002, regardless of 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 multispecies model that allowed species-specific change points (Fig. 7). Similar results were obtained from multispecies 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 ($\Pr(k_j > 0) > 0.75$) had not excluded variables that could explain the post-2000 declines, we refitted covariate-conditioned change point models including all variables with $\Pr(k_j > 0) > 0.5$ (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 six variables per species; see Mac Nally et al. 2010 for details). With one possible exception (detailed in *Species-specific results: Striped bass* below), inclusion of additional variables had no substantive effects on posterior probabilities of post-2000 change points in single- or in multispecies models.

Water clarity emerged as a likely predictor of the abundance of delta smelt, longfin smelt, and striped bass, but the other variables with $\Pr(k_j > 0) > 0.75$ were unique to each species (Table 2). No species had more than two variables with $\Pr(k_j > 0) > 0.75$. All of the covariates with $\Pr(k_j > 0) > 0.75$ 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 (Figs. 3C, 4C, 5C, and 6C and 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 ($\Pr(k_j > 0) > 0.75$; 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 ($\beta = -0.25$; Table 2) implies that an increase of one standard deviation 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

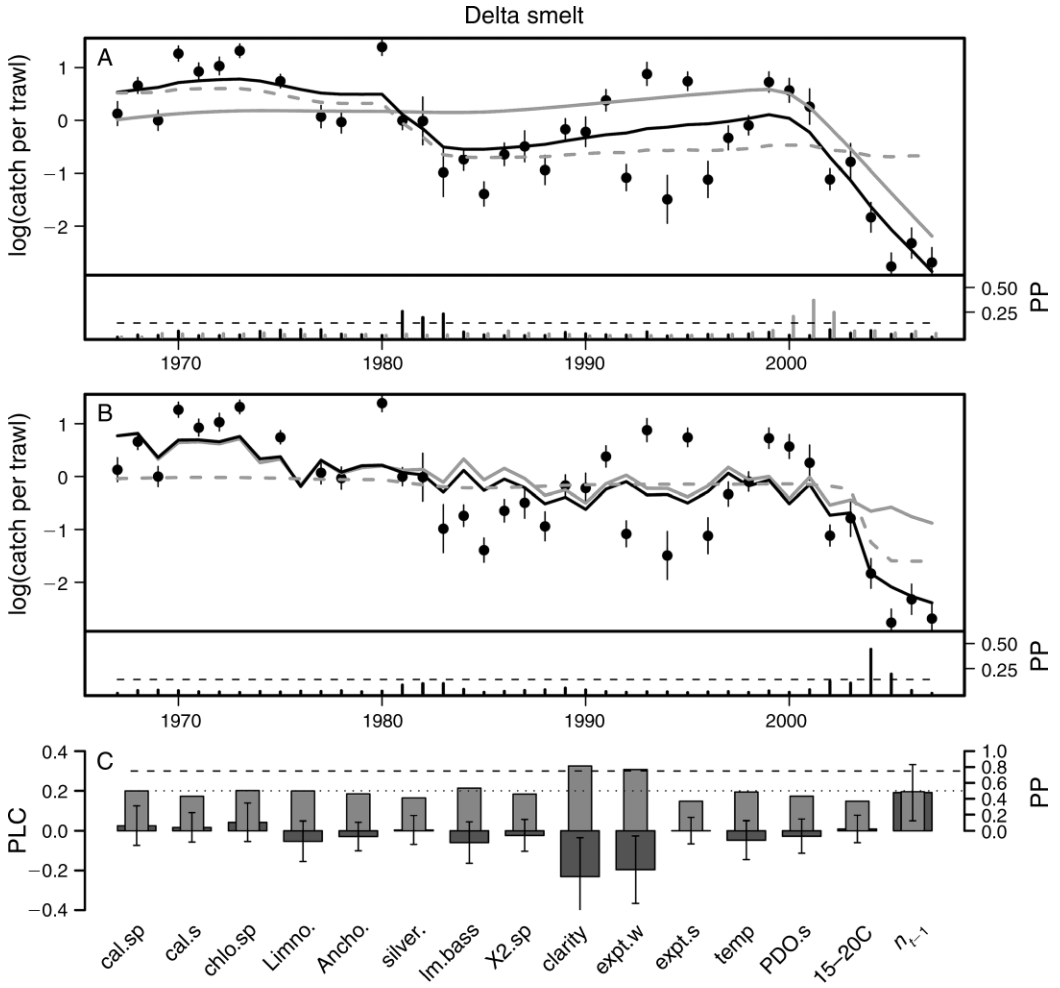

FIG. 3. (A) Results of the trend model (Eq. 2) for delta smelt. The fitted trend is shown as a black line, and observed values [log(catch per autumn trawl), mean ± SE] are shown as data points. Intercept (α_t) values are shown as dashed gray lines, and the trend component [$f_t(t)$] is shown as a solid gray line. The lower panel shows posterior probabilities (PP) of step changes (black) or trend changes (gray) in each year for the trend model (Eq. 2). (B) Results of the 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 gray line, and the covariate component [f(water clarity) + f(winter exports), where $f(\ )$ is a linear spline] as a solid gray line. The posterior probabilities of step changes (abrupt changes unexplained by covariates) for each year are shown in the lower panel. (C) Results of the covariate selection model (Eq. 5) for delta smelt. Posterior probabilities of variable inclusion (light gray bars, right axis) and posterior mean (±SE) linear coefficients (PLC; dark gray bars, left axis) are shown for each candidate predictor. The variable n_{t-1} is the previous year's abundance; see Table 1 for explanations of other covariate abbreviations. Mean linear coefficients were calculated as the mean slope of the fitted linear-spline model over the data range. In all panels, the 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 (panels A and B) or for a variable having an effect on abundance (panel C). In panel (C) the prior probability of inclusion (0.5) is shown as a dotted line.

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 multispecies model (Fig. 7). The mean effect of winter exports was slightly less negative in the multispecies model than in the single-species model (Table 2) because the multispecies 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 ($\Pr(k_j > 0) > 0.75$). 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

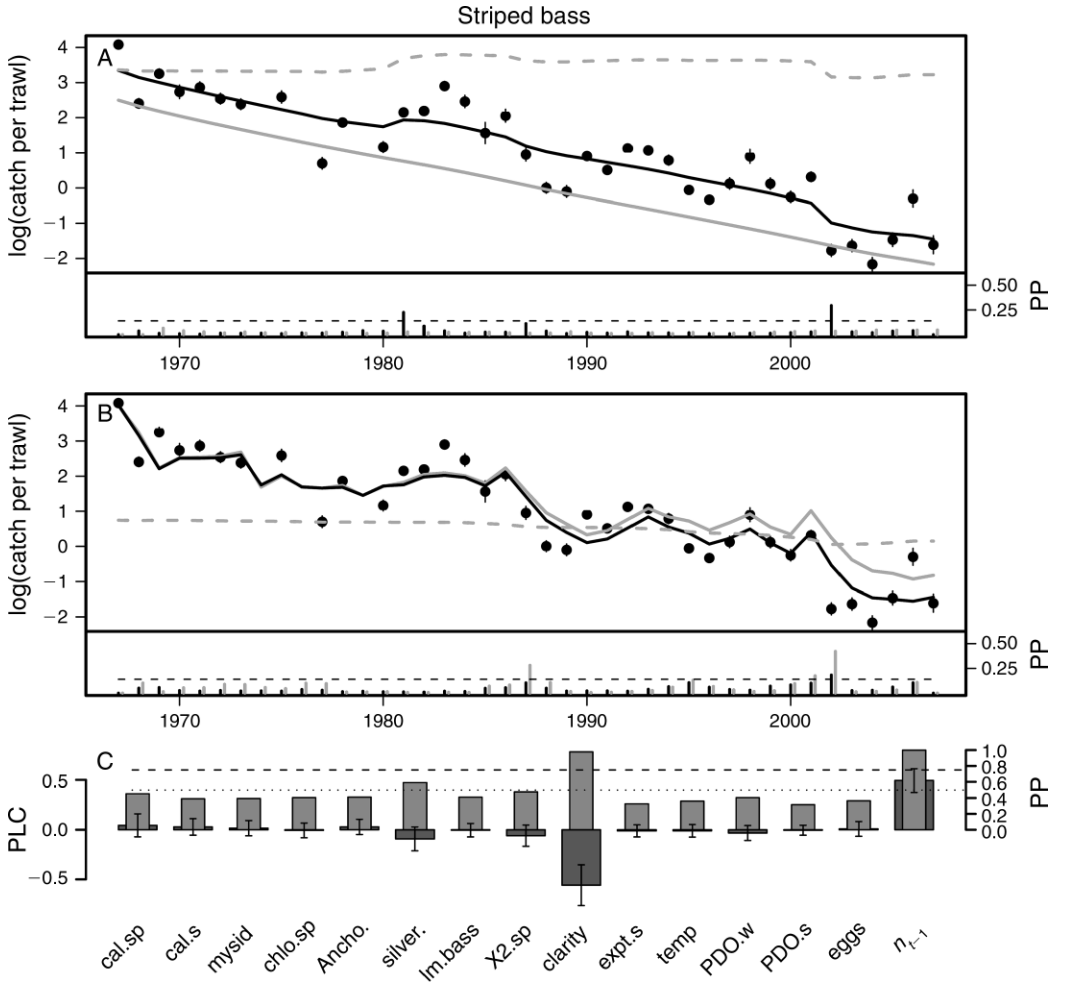

FIG. 4. Results of the models for striped bass. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(water clarity) + $\rho \log(n_{t-1})$. The gray bars in panel (B) show the posterior probabilities of change points in each year if $\rho = 0$; $\rho \log(n_{t-1})$ is the temporal autocorrelation term in Eq. 6 (see *Statistical analyses: Covariate-conditioned change point model*).

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 multispecies 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 multispecies 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 1988–1992.

Striped bass (age-0).—In the variable-selection model for striped bass, water clarity and the autocorrelation term had $\Pr(k_j > 0) > 0.75$. 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

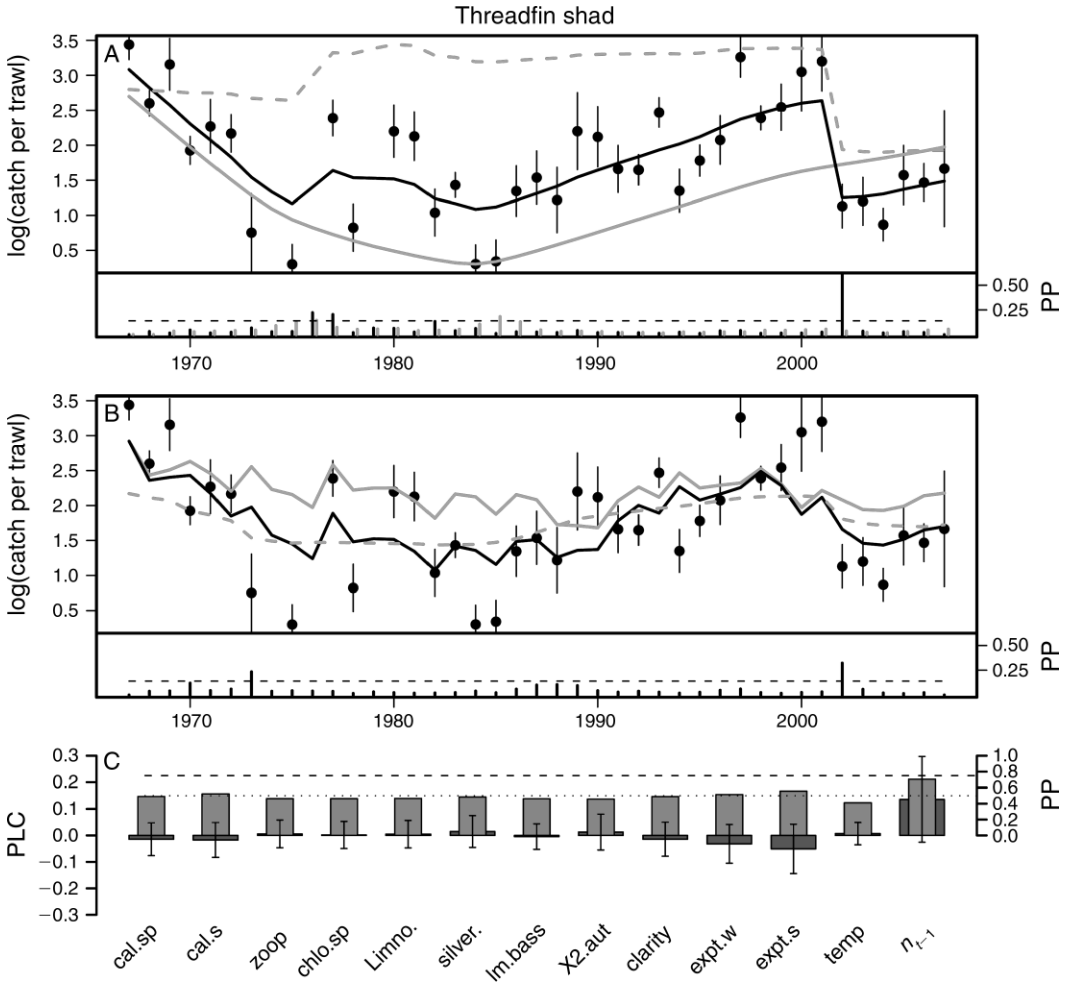

FIG. 5. Results of the models for threadfin shad. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(winter exports) + f(spring exports), and the dashed gray line represents the time-dependent intercept α_t plus a nonlinear trend $f(t)$.

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). 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. Figs. 4B and 7).

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 $\Pr(k_j > 0) > 0.75$ 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 ($R^2 =\leftarrow$ 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 multispecies models with and without time included as a covariate. An

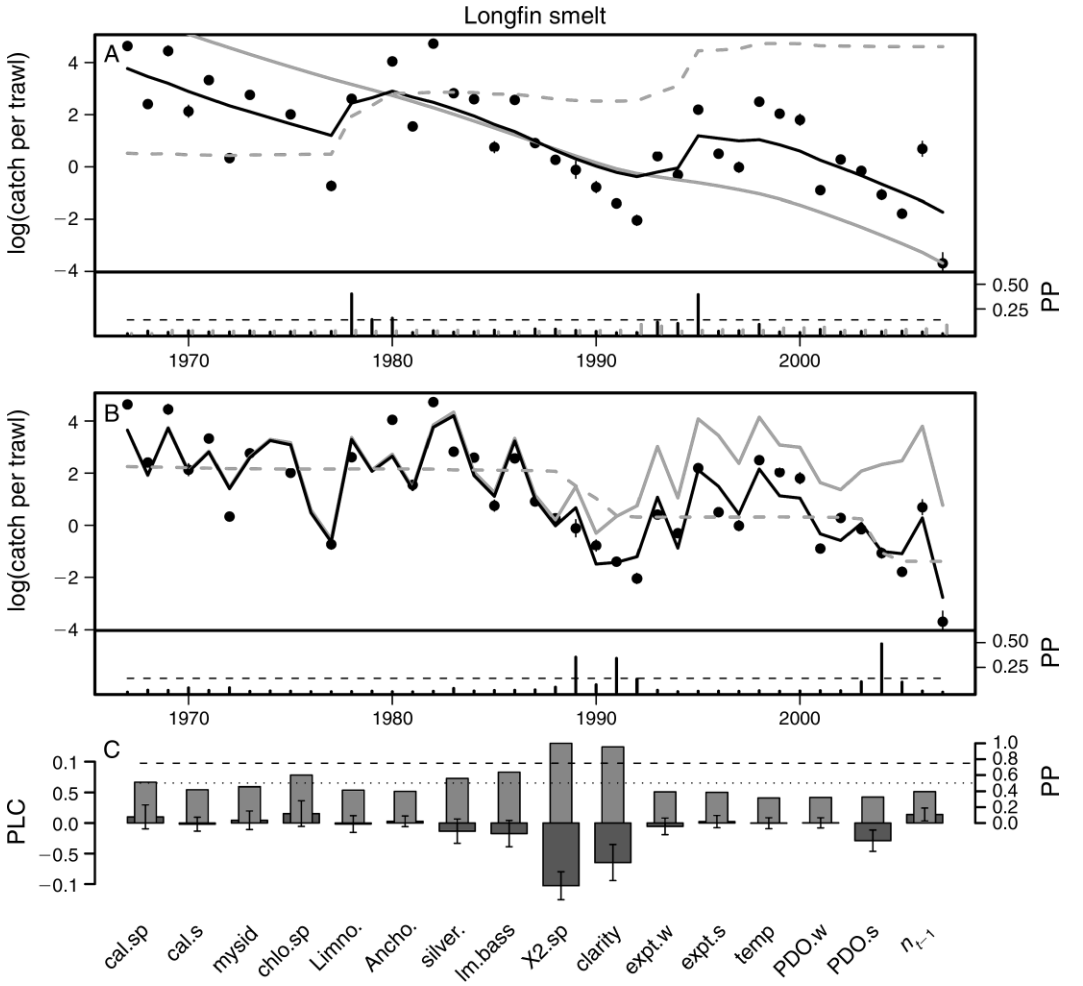

FIG. 6. Results of the models for longfin smelt. Panel details are as in Fig. 3. In panel (B), the covariate component (solid gray line) represents f(water clarity) + f(spring X2), but f(water clarity) was near zero, and including only f(spring X2) results in essentially the same figure as this.

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 Figs. 5B and 7). The estimated relationship between winter exports and threadfin was weak in all models (Table 2), especially in the multispecies 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 multispecies 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,

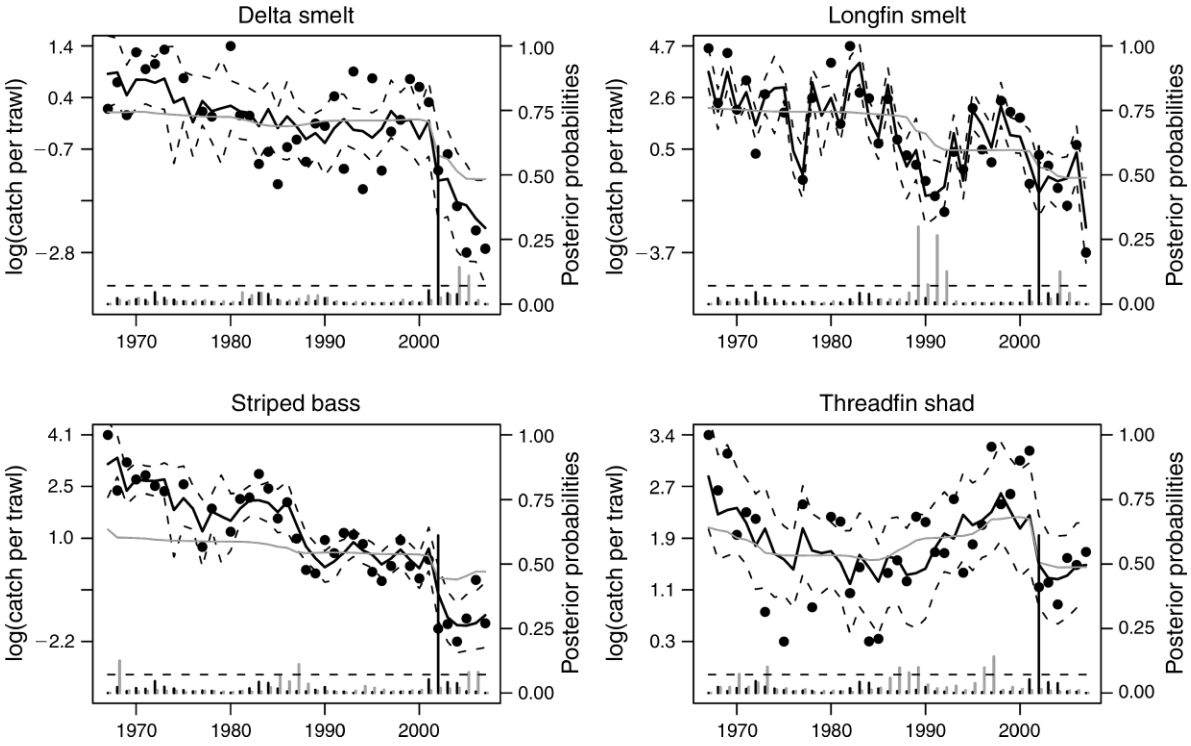

FIG. 7. Abundance [log(catch per trawl)] with fitted values (solid black lines; dashed lines are 95% credible intervals) and intercept parameters (gray solid lines) for delta smelt, longfin smelt, striped bass, and threadfin shad in the multispecies change point model. Intercept parameter =~~species-specific~~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

were moderately reduced (Table 2). A similar reduction in the estimated effect of winter exports in the multispecies model was observed for threadfin shad. The increased probability of unexplained declines in 2002 and reduced covariate effects in the multispecies model, relative to the single-species models, reflect differences in the amounts of data (evidence) used to fit the different models. Combining data from all species in the multispecies model strengthened the evidence 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 1989–1991. These declines may be related to the effects of the introduced (ca. 1987) clam *Corbula amurensis*, which caused an ongoing decrease of ~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 MAR model of this system (see Mac Nally et al. 2010). 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

TABLE 2. Summary of covariate effects in models of annual abundance of four species of pelagic fishes in the San Francisco Estuary.

Covariate	Pr	Single-species model		R^2
		Mean slope (SD)	95% CI	
Delta smelt				0.65
Water clarity	0.81	−0.24 (0.29)	(−0.85, 0.29)	
Winter exports	0.77	−0.25 (0.18)	(−0.60, 0.09)	
Longfin smelt				0.88
Spring X2	1.00	−1.25 (0.18)	(−1.61, −0.88)	
Water clarity	0.96	−0.15 (0.43)	(−1.05, 0.58)	
Striped bass				0.88
Water clarity	0.99	−0.59 (0.24)	(−1.04, −0.06)	
ρ	0.98	0.38 (0.17)	(0.05, 0.69)	
Threadfin shad				0.45
Winter exports	0.51†	−0.14 (0.19)	(−0.52, 0.25)	
Spring exports	0.59†	−0.22 (0.14)	(−0.50, 0.06)	

Notes: We used a variable selection model (Eq. 5) to select covariates and included the covariates in subsequent models if their posterior probability of inclusion (Pr) exceeded 0.75 (see Figs. 3, 4, 5, and 6 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 three knots (changes in slope). All fitted splines were monotonic, and departures from linearity generally were moderate and are described in the "functional response" column. 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_t's in Eq. 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. Covariate ρ is the autocorrelation coefficient in Eq. 6.

† 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 *Results: Species-specific results* and Appendix).

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. 2009). 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 et al. 2004) and can mediate predator–prey interactions (Abrahams and Kattenfeld 1997, Gregory and Levings 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 nonlinear 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.

TABLE 2. Extended.

Multispecies model			
Mean slope (SD)	95% CI	R^2	Functional response
		0.63	
−0.24 (0.26)	(−0.74, 0.30)		single-species model: weak at values >2 SD from mean, multispecies model: stronger at values > 1 SD
−0.22 (0.17)	(−0.55, 0.11)		weaker at values < −1 SD
		0.85	
−1.20 (0.18)	(−1.55, −0.83)		stronger at values > mean
−0.27 (0.41)	(−1.14, 0.48)		stronger at values > 1 SD
		0.89	
−0.57 (0.27)	(−1.06, −0.03)		linear
0.40 (0.13)	(0.11, 0.66)		
		0.46	
−0.10 (0.18)	(−0.45, 0.28)		single-species model: weak at values < mean, multispecies model: linear
−0.23 (0.14)	(−0.48, 0.03)		single-species model: weaker at values < −1.5 SD, multispecies model: linear

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 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. 2010). In the MAR analysis, abiotic variables explained 50% more variation than did trophic interactions. Trophic interactions were still important (Mac Nally et al. 2010), 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 such as 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.

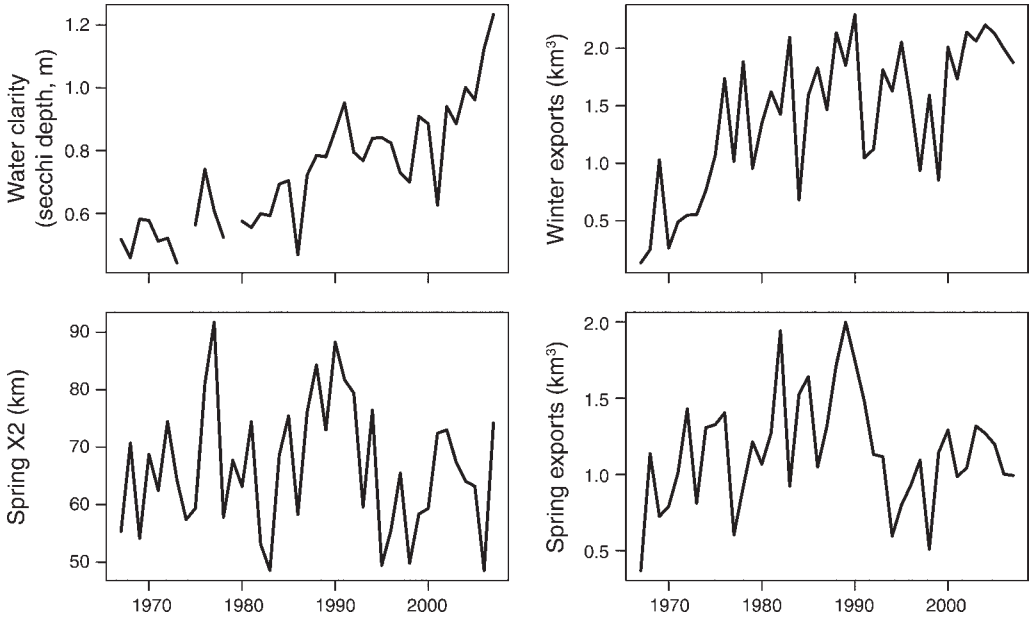

FIG. 8. Trends in covariates used in covariate-conditioned change point models. See Table 1 for explanations of covariates.

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 nonparametric trend models with change points for step and trend changes (Eq. 2), nonlinear variable selection models (Eq. 5), nonlinear 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. 2010), and interactions among covariates were not investigated. Some preliminary work (J. R. Thomson, *unpublished data*) 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. Multispecies 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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APPENDIX

Details of prior distributions used in change point and associated regression models (*Ecological Archives* A020-051-A1).

SUPPLEMENT

WinBUGS and R code to fit change point and variable selection models (*Ecological Archives* A020-051-S1).