

Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR)

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Abstract. Four species of pelagic fish of particular management concern in the upper San Francisco Estuary, California, USA, have declined precipitously since ca. 2002: delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*). The estuary has been monitored since the late 1960s with extensive collection of data on the fishes, their pelagic prey, phytoplankton biomass, invasive species, and physical factors. We used multivariate autoregressive (MAR) modeling to discern the main factors responsible for the declines. An expert-elicited model was built to describe the system. Fifty-four relationships were built into the model, only one of which was of uncertain direction a priori. Twenty-eight of the proposed relationships were strongly supported by or consistent with the data, while 26 were close to zero (not supported by the data but not contrary to expectations). The position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow) and increased water clarity over the period of analyses were two factors affecting multiple declining taxa (including fishes and the fishes' main zooplankton prey). Our results were relatively robust with respect to the form of stock–recruitment model used and to inclusion of subsidiary covariates but may be enhanced by using detailed state–space models that describe more fully the life-history dynamics of the declining species.

Key words: Bayesian analysis; delta smelt; expert models; longfin smelt; Sacramento River, California, USA; San Joaquin River, California, USA; striped bass; threadfin shad; threatened species; water management.

INTRODUCTION

Estuaries, especially those associated with large rivers near major cities, are among the ecosystems most adversely affected by land use change (Nichols et al. 1986). Impacts of human actions in all upstream watersheds (catchments) are concentrated in the estuaries (Kennish 2002, Townend 2004). Diversion of water affects the location of boundaries between fresh, brackish, and saline water (Drinkwater and Frank

1994, Gillanders and Kingsford 2002, Gleick 2003). Large settlements often are located along shorelines, which convey contaminants and effects of boating and fishing to estuarine systems (Dauer et al. 2000). Shipping has led to introductions of many aquatic invasive species (Bollens et al. 2002, Williams and Grosholz 2008). Climate change will affect interactions between oceans and estuaries and will reduce catchment inflows in many regions (Scavia et al. 2002, Vicuna and Dracup 2007, Cai and Cowan 2008, Schindler et al. 2008).

The San Francisco Estuary is an archetype of a stressed estuarine system (Kimmerer et al. 2005a). The social, economic, and ecological effects of freshwater flows and diversions throughout the San Francisco Estuary have received much attention. Some 25 million Californians and 12 000 km² of agricultural land rely on water diversions from the delta created by the Sacramento and San Joaquin rivers. Annual agricultural

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revenue from California's Central Valley, which accounts for about half of the production of fruits and vegetables in the United States, frequently approaches US\$15 billion.

Populations of many aquatic species in the estuary have declined since extensive human activities began in the mid-1800s (Bennett and Moyle 1996, Brown and Moyle 2005). However, conflicts over water management recently have intensified because of the apparently precipitous decline in four species of pelagic fish (delta smelt [*Hypomesus transpacificus*], longfin smelt [*Spirinchus thaleichthys*], striped bass [*Morone saxatilis*], and threadfin shad [*Dorosoma petenense*] since ca. 2002 (Thomson et al. 2010). Delta smelt was listed as threatened under the U.S. and California Endangered Species Acts in 1993. 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, although a petition for federal listing was declined. Striped bass was deliberately introduced to the Sacramento–San Joaquin Delta from the east coast of the United States in 1879 and supports a sport fishery (Moyle 2002). Threadfin shad was introduced into California reservoirs as a forage fish in 1954 and spread to the Delta (Moyle 2002, Feyrer et al. 2009).

To date, models and statistical analyses to identify mechanisms causing fish declines in the San Francisco Estuary generally have been on a species-by-species basis (Jassby et al. 1995, Kimmerer et al. 2001, Bennett 2005). These efforts suggest that several abiotic factors (e.g., water flows, salinity, turbidity), bottom-up biotic effects (e.g., zooplankton abundances, invasion of a filter-feeding, non-native clam [*Corbula amurensis*]), and top-down factors (e.g., incidental mortality associated with water diversions to pumping facilities) may play important roles. However, the relative importance of these factors remains unclear (Sommer et al. 2007). Identification of processes causing declines is critical because possible solutions include major investments in infrastructure, changes in water management, and rehabilitation of species' habitats, which would cost billions of dollars.

Although detailed analyses of the population dynamics of any one declining species are valid, it is plausible that more insight might be gained through multivariate analyses that consider community dynamics, including direct and indirect effects of interacting species and abiotic factors. These analyses might yield inferences on the biotic and abiotic factors that best explain patterns of abundance for multiple species in the community and on the relative influences of density dependence, among-species interactions, and abiotic factors on species abundances.

We used a multivariate statistical technique called multivariate autoregressive modeling (MAR) (Ives et al. 2003) with 40 years of data for pelagic fishes and their principal prey within the upper San Francisco Estuary.

In a manner similar to path analysis (Shipley 1997), MAR uses time series data for multiple taxa to estimate the degree of association between the different taxa as well as between covariates and each taxon. Multivariate autoregressive modeling includes autoregressive terms for each species' abundance. Ives et al. (2003) provided a detailed introduction to the underlying theory and assumptions of MAR along with methods for estimating model parameters. Multivariate autoregressive modeling has been used in analyses of community dynamics in lakes in Wisconsin (Ives et al. 2003), Lake Washington (Hampton and Schindler 2006), and Lake Baikal (Hampton et al. 2008).

We developed a Bayesian implementation of MAR. Bayesian methods allow propagation of and account for multiple sources of uncertainty in complex models (Punt and Hilborn 1997) and allow great flexibility in model structure (Cressie et al. 2009). The Bayesian MAR modeling is a complementary approach to methods we used in a companion paper, which presented a Bayesian change point analysis (Thomson et al. 2010). The two methods were developed in tandem to evaluate whether the different strengths of the MAR and change point analyses provided similar inferences about factors potentially underlying causes of declines in the fish species. Multivariate autoregressive modeling is based on a food web structure, which allows both direct and indirect influences on the focal species (fish) to be represented. Moreover, MAR models the dynamics of all species (including prey) simultaneously. It is based on linear relationships (on a log-abundance scale), both within the food web and with covariates, over the entire time period.

Our implementation of MAR is underlain by an expert-elicited model, which draws on expert knowledge to specify whether particular trophic or covariate effects may be influential. The change point analysis is not embedded in a food web context, although availabilities of prey taxa can be used as covariates, but it does explicitly employ time dependence and nonlinearity in covariate relationships between log-abundances of the focal species and covariates. The change point method uses Bayesian variable selection (Green 1995) so that relationships do not need to be specified a priori. Both individual-species (species-specific model parameters) and multiple-species (common hyper-parameter distributions) versions of the change point analyses were implemented (Thomson et al. 2010), with the latter having some overlap, therefore, with the MAR analyses.

Here, we describe the upper San Francisco Estuary, the four species of fish on which we focused and their principal prey, and the set of covariates included in the MAR model. Multivariate autoregressive models are heavily parameterized because they describe many among-taxa interactions and relationships to covariates. Therefore, we developed an expert-elicited, circumscribed model that reduced the number of parameters to be estimated. We review the relative importance of

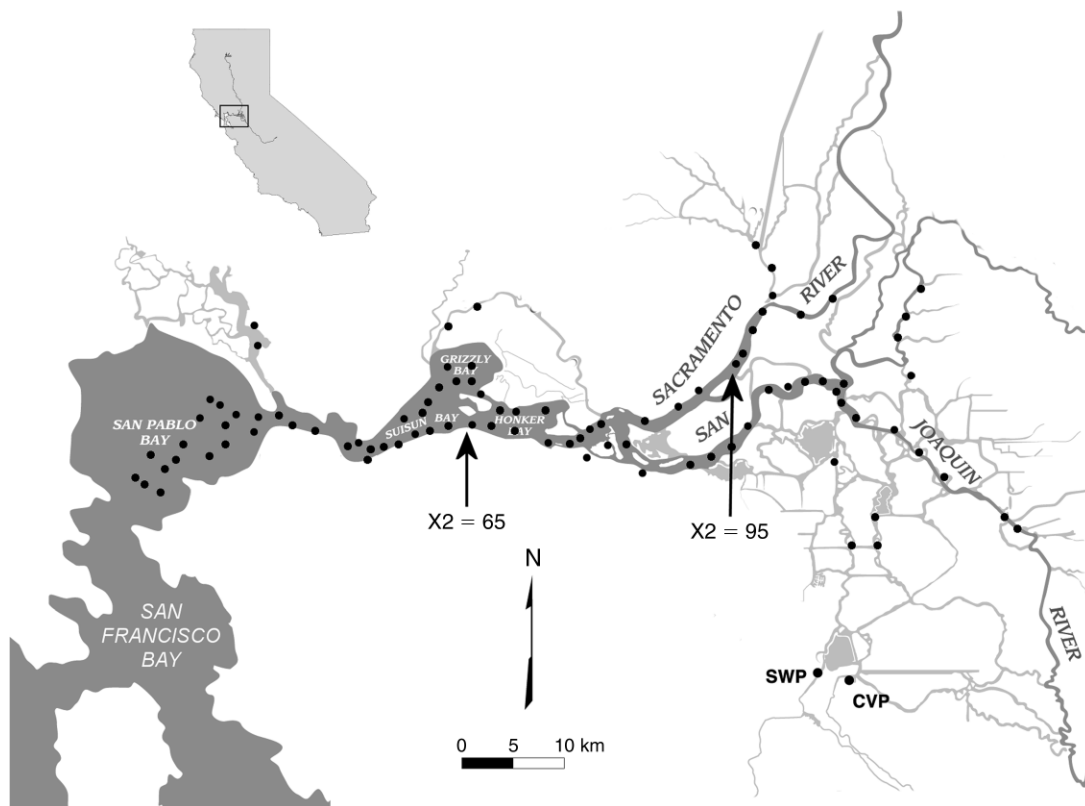


FIG. 1. Location and physiography of the upper San Francisco Estuary, California, USA. The solid circles denote sampling locations of the autumn midwater trawl surveys; arrows indicate two representative positions of the 2‰ isohaline (X2); SWP (State Water Project) and CVP (Central Valley Project) are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

different factors in driving the temporal dynamics of our four declining fish species and comment on the usefulness and limitations of MAR models. Last, we comment on the agreement or otherwise between the MAR and change point approaches.

METHODS

The San Francisco Estuary

The San Francisco Estuary consists of three major regions: San Francisco Bay, the most seaward region; Suisun Bay, an intermediate brackish region; and the generally freshwater Sacramento–San Joaquin Delta (Fig. 1). The watershed has wet winters and dry summers. The Delta is the core of a massive system of dams and canals that store and divert water from the estuary for agricultural, industrial, and domestic use throughout California (Nichols et al. 1986). The water diversion facilities export ~30% of the annual freshwater flow into the Delta, although that percentage has exceeded 60% during many recent summers. Regulations, 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.

Response variables: declining fish and their principal prey

Delta smelt is endemic to the San Francisco Estuary and reaches 60–70 mm standard length (SL) (Bennett 2005), feeding on zooplankton, mainly calanoid copepods, throughout life. The delta smelt is weakly anadromous, migrating between the brackish waters of Suisun Bay and the freshwaters of the Delta. Upstream migration begins in the late autumn or early winter and spawning occurs from March through May in freshwater. Most delta smelt spawn ~12 months after hatching, with a small percentage surviving for another year to spawn. Young delta smelt move downstream in early summer and remain in the low-salinity zone (0.5–10‰) until they migrate for spawning.

Longfin smelt is native to the San Francisco Estuary. The species usually reaches 90–110 mm SL (Moyle 2002, Rosenfield and Baxter 2007) and is anadromous. It spawns at age 2 yr in freshwater in the Delta from 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 mysids and amphipods as young and adults.

Striped bass is a potentially large (>1 m), potentially long-lived (>10 yr) anadromous species. Females begin

TABLE 1. Definitions of variables used in the multivariate autoregressive modeling, years for which data were available, and ranges of values for variables.

Variable	Years (missing)	Range	Definition
Response variables			
Delta smelt (<i>Hypomesus transpacificus</i>)	1967–2007 (3)	0.06–4.02	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Longfin smelt (<i>Spirinchus thaleichthys</i>)	1967–2007 (3)	0.03–113.16	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Striped bass (<i>Morone saxatilis</i>)	1967–2007 (3)	0.12–59.38	autumn (Sep–Dec) midwater trawl, mean age-0 catch per trawl
Threadfin shad (<i>Dorosoma petenense</i>)	1967–2007 (3)	1.36–31.21	autumn (Sep–Dec) midwater trawl, mean total catch per trawl
Calanoid copepods, spring	1972–2007 (1)	0.98–43.87	mean biomass of calanoid copepodites and adults during spring (Mar–May) in low-salinity zone
Calanoid copepods, summer	1972–2007 (1)	2.93–27.62	mean biomass of calanoid copepodites and adults during summer (Jun–Sep) in low-salinity zone
Mysids	1972–2007 (0)	0.42–35.05	mean biomass of mysid shrimp during Jun–Sep in low-salinity zone
Covariates			
Northern anchovy (<i>Engraulis mordax</i>)	1980–2006 (1)	0.22–490.42	mean catch per trawl of northern anchovy in the Bay Study midwater trawl (Jun–Sep) in the low-salinity zone
“Other zooplankton” in spring	1972–2006 (0)	3.79–56.86	mean biomass of other zooplankton (not including crab and barnacle larvae, cumaceans) during spring (Mar–May) in the freshwater zone
Spring chlorophyll <i>a</i> (freshwater zone)	1972–2006 (0)	2.35–43.54	mean chl <i>a</i> (mg/m ³) during spring (Mar–May) in freshwater zone
Spring chlorophyll <i>a</i> (low-salinity zone)	1975–2006 (0)	1.12–21.32	mean chl <i>a</i> (mg/m ³) during spring (Mar–May) in low-salinity zone
Summer chlorophyll <i>a</i>	1975–2006 (0)	1.23–20.15	mean chl <i>a</i> (mg/m ³) during summer (Jun–Sep) in low-salinity zone
Cyclopoid copepod <i>Limnoithona tetraspina</i>	1972–2006 (0)	0–7.78	mean biomass of <i>Limnoithona</i> copepodites and adults during summer (Jun–Sep) in low-salinity zone
Inland silverside (<i>Menidia beryllina</i>)	1994–2006 (0)	19.88–116.54	mean catch per seine haul of inland silverside in the USFWS survey during Jul–Sep (for stations within the delta)
Largemouth bass (<i>Micropterus salmoides</i>)	1994–2006 (0)	0.02–8.00	mean catch per seine haul of largemouth bass in the USFWS survey during Jul–Sep (for stations within the delta)
Spring X2 (isohaline)	1967–2006 (0)	48.53–91.74	mean Mar–May position of the 2‰ isohaline (X2)
Autumn X2 (isohaline)	1967–2006 (0)	60.24–93.18	mean Sep–Dec position of the 2‰ isohaline (X2)
Water clarity	1967–2006 (0)	0.44–11.00	mean Secchi depth (m) for the autumn midwater trawl survey
Winter exports	1967–2006 (0)	0.13–12.00	total volume of water (km ³) exported by the California State Water Project and Central Valley Project during Dec–Feb
Spring exports	1967–2006 (0)	0.37–13.00	total volume of water (km ³) exported by the California State Water Project and Central Valley Project during Mar–May
Invasive clam <i>Corbula amurensis</i>	1967–2006 (0)	0–1	binary variable for presence (1987–2006, 1) or absence (1967–1986, 0)
Duration of spawning window for delta smelt	1975–2007 (0)	24–85	no. days for which mean temperature was between 15° and 20°C, † mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta
Mean summer water temperature	1967–2006 (0)	20.45–23.65	mean water temperature (°C), mean of five continuous monitoring stations throughout Suisun Bay and the Sacramento–San Joaquin Delta during Jun–Sep

Notes: Mean catch per trawl was measured in terms of individuals. Biomass was measured as mg C/m³. The freshwater zone was determined to be <0.5‰. 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.

† Range of water temperatures that best induce spawning by delta smelt (15°C) and limit larval survivorship (20°C).

to spawn at age 4 yr in the Sacramento River and, to a lesser extent, in the San Joaquin River, from April through June. Eggs drift with the current as they develop and hatch. Larvae drift into the low-salinity zone where they grow, later dispersing throughout the estuary. Adults occur primarily in saline waters of the estuary

and 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 typically is <100 mm total length and primarily inhabits freshwater. It switches between filter- and particle-feeding, consuming phytoplankton, zoo-

plankton, and detritus. Most threadfin shad spawn in their second summer, 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.

While other fish and plankton groups might be included in our model as response variables, we chose to limit our analysis to species of zooplankton that are especially important for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad. Adult and juvenile (copepodites) calanoid copepods have different relationships with the fish in spring and summer, so we considered the two life stages as different “taxa” in our models. Mysid shrimps were regarded as most important to the fishes in the mid to late summer (Table 1).

Covariates

The covariates used in the MAR (Table 1) relate to factors thought to be important for one or more of the response variables (Table 2). Covariates included fish species that are potential competitors or predators of the four declining fish species (possibly at only certain life-history stages), food for the latter fishes or their crustacean prey (including phytoplankton), competitors (*Limnoithona*) or predators (*Corbula*) of the crustaceans, the primary surrogate of the fishes’ habitat (X2) in spring and autumn, amounts of water extracted from the Delta in winter and spring, water clarity (measured using Secchi discs), and two water temperature variables (duration of the delta smelt spawning window, mean summer water temperature).

The expert model (Table 2) was based on extensive, long-term knowledge and experience of several of the authors (W. J. Kimmerer, F. Feyrer, W. A. Bennett, L. Brown, S. D. Culberson, G. Castillo), and justifications for expected relationships were drawn from the literature. Although Bayesian model selection (Green 1995) might have been incorporated into the MAR model, as was done for the complementary change point analyses (Thomson et al. 2010), we believe that there is didactic value in concentrating on the evidential support for the expert-elicited model.

STATISTICAL ESTIMATION

MAR: Gompertz dynamics

We used a variant of a MAR model (Ives et al. 2003) to represent dynamics of the response variables. We represented population dynamics with the Gompertz model (Dennis et al. 2006). We began with a deterministic version of the Gompertz model (Reddingius 1971):

$$n_{i,t} = n_{i,t-1} \exp(\gamma_i + \delta_i \ln n_{i,t-1}) \tag{1}$$

in which $n_{i,t}$ is abundance of species i at time t , $n_{i,t-1}$ is abundance of species i at time $t - 1$, γ_i is the intrinsic rate of population growth for species i , and δ_i , which has been interpreted as the degree of density dependence.

We extended Eq. 1 first by allowing propagation for longer lags (up to L years prior to the current year), that is, an L th-order Gompertz model (Zeng et al. 1998):

$$n_{i,t} = n_{i,t-1} \exp(\gamma_i + \sum_{l=1}^L \delta_{il} \ln n_{i,t-l}). \tag{2}$$

It is possible that the γ_i may vary, so we allowed linear time dependence: $\gamma_i(t) = \gamma_{i,0} + \gamma_{i,1}t$. We expected the $\gamma_{i,1}$ parameters to be <0 given the declines in the abundances of the fishes. Taking logarithms, setting $x_{i,t} = \ln n_{i,t}$, and allowing species-specific lags (L_i), we have

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l}. \tag{3}$$

Interspecific interactions among the seven taxa included as response variables were incorporated by appending terms relating to the previous year $\beta_{ij}x_{j,t-1}$, excluding self-terms:

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j \neq i}^J \beta_{ij} x_{j,t-1}. \tag{4}$$

We included effects of covariates u_k through α coefficients for the current year t :

$$x_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j \neq i}^J \beta_{ij} x_{j,t-1} + \sum_{k=1}^K \alpha_{ik} u_{k,t}. \tag{5}$$

MAR implementation

We used a Bayesian framework for implementing the model. There are many advantages to so doing. First, propagation of measurement uncertainties is straightforward using hierarchical models. Second, missing data are easily accommodated and estimated within the same process by which the parameters estimated are made, rather than a clumsier two-stage imputation–estimation approach. Third, we believe that the prior expectations, which also are easily implemented in a Bayesian framework, are critical encapsulations of the state of knowledge before the modeling was undertaken and need to be made explicit, as we have done.

We implemented Eq. 5 using the following model in WinBUGS, version 1.4 (Spiegelhalter et al. 2003):

$$z_{i,t} \sim \mathcal{N}(x_{i,t}, \omega_{i,t}^2) \quad x_{i,t} \sim \mathcal{N}(\mu_{i,t}, \sigma_i^2) \quad c'_{k,t} \sim \mathcal{N}(u_{k,t}, \zeta_k^2)$$

$$\mu_{i,t} = x_{i,t-1} + \gamma_i(t) + \sum_{l=1}^{L_i} \delta_{il} x_{i,t-l} + \sum_{j=1, j \neq i}^J \beta_{ij} x_{j,t-1} + \sum_{k=1}^K \alpha_{ik} u_{k,t} \tag{6}$$

(\mathcal{N} denotes the normal distribution). The model states

TABLE 2. Matrix of effects included in the model with explanations.

Response variable or covariate	Response variable							Explanation
	DS	LFS	SB	TFS	CA-SP	CA-SU	MYS	
Delta smelt (DS)					-	-		Calanoid copepods are consumed by delta smelt (Hobbs et al. 2006).
Longfin smelt (LFS)					-	-	-	Calanoid copepods and mysids are consumed by longfin smelt (Feyrer et al. 2003).
Striped bass (SB)					-	-	-	Calanoid copepods and mysids are eaten by young striped bass (Feyrer et al. 2003, Bryant and Arnold 2007).
Threadfin shad (TFS)								Threadfin shad consume phytoplankton and copepods but are most abundant in freshwater (Turner and Kelley 1966, Feyrer et al. 2007).
Calanoids, spring (CA-SP)	+	+	+					Key food for young fish in spring.
Calanoids, summer (CA-SU)	+	+	+				+	Key food for young fish in summer; mysids consume calanoids (Siegfried et al. 1979, Siegfried and Kopache 1980).
Mysids (MYS)		+	+				-	Key food for young longfin smelt and striped bass in summer.
Anchovy					-	-	-	Biomass dominant, consumes all plankton (Kimmerer 2006).
Other zooplankton				+				Threadfin shad consume zooplankton in freshwater (Turner and Kelley 1966).
Chlorophyll <i>a</i> , spring, freshwater					+			
Chlorophyll <i>a</i> , spring, low-salinity zone					+		+	Calanoids eat microplankton, including phytoplankton (Gifford et al. 2007) and respond positively to phytoplankton blooms (Kimmerer et al. 2005b).
Chlorophyll <i>a</i> , summer, low-salinity zone						+	+	Mysids eat phytoplankton and small zooplankton (Siegfried and Kopache 1908).
<i>Limnoithona tetraspina</i>							-	Indirect effect through depression of food resource (ciliates; not measured) (Bouley and Kimmerer 2006, Gifford et al. 2007).
Inland silverside	-				-	-		Silversides consume copepods and potentially delta smelt eggs and larvae (Bennett and Moyle 1996).
Largemouth bass	-		-	-				Potentially important predator on small fish in freshwater (Nobriga and Feyrer 2008).
X2, spring		-	-		+/-		-	Effects of spring X2 on subsequent abundance in the following autumn (Jassby et al. 1995, Kimmerer et al. 2009).
X2, autumn	-	-	-					X2 affects surface area available for fish through salinity distribution (Feyrer et al. 2007).
Water clarity	-	-	-	-				Turbidity favors all fish at various life-history stages by offering increased protection from predators (Feyrer et al. 2007, Nobriga and Feyrer 2008, Kimmerer et al. 2009).
Export flow, winter	-	-						Adult smelt are entrained by pumping facilities during winter (Baxter et al. 2008, Kimmerer 2008).
Export flow, spring	-	-	-	-				Juvenile and adult smelt and shad and juvenile striped bass are entrained by pumping facilities during spring (Baxter et al. 2008).
<i>Corbula amurensis</i>					-	-		Nauplius larvae of copepods are consumed by <i>Corbula</i> (Kimmerer et al. 1994).
Spawning window	+							Spawning window for delta smelt is constrained by temperature (Bennett 2005).
Mean summer water temperature	-							Delta smelt are negatively influenced by high water temperatures, reducing time spent in the freshwater Delta (Swanson et al. 2000).

Notes: A “+” denotes that the covariate was expected to exert a positive influence on the response variable (e.g., food source). A “-” indicates that the covariate was expected to have a negative influence on the response variable (e.g., by consumption). All null entries were deemed likely to be unimportant by expert knowledge. The abbreviations “X2” refers to the position of the 2‰ isohaline (a measure of the physical response of the estuary to freshwater flow).

that the (ln-transformed) observed values ($z_{i,t}$) represent the true values ($x_{i,t}$). The former have observation errors, which are included by use of (ln-transformed) unobserved values ($x_{i,t}$) and observation errors, $\omega_{i,t}^2$. The observation errors were estimated from SEs of mean values for the response variables for each time period.

Given that the $z_{i,t}$ were ln-transformed, we used a Taylor functional expansion to approximate the ln-transformed SEs [$SE(\ln(\bar{n})) \approx SE(\bar{n})/\bar{n}$] (Seber 1973, Stuart and Ord 1987). Process variances (σ_i^2) were allowed to be species-specific and were implemented with priors on σ_i of $U(0.01, 10)$ (Gelman 2005) ($U = \text{Uniform}$). The true,

unobserved values ($\mu_{i,t}$) are driven by the population dynamic parameters, trophic interactions, and covariates as described by the MAR model (Eq. 5).

Observed covariates $c_{k,t}$ were standardized for all available years of data (subtract mean \bar{c}_k , divide by standard deviations SD_k over all years, $c'_{k,t} = (c_{k,t} - \bar{c}_k) / SD_k$). Standardizing is helpful for model convergence and for equalizing numerical ranges among different scales of measurement. Uncertainties in covariate measurements (within-year SEs) correspondingly were scaled by the interannual standard deviations (i.e., $SE_{k,t} / SD_k$). The model specifies that the true (standardized) covariate values ($u_{k,t}$) are related to the observed standardized values ($c'_{k,t}$) but include the covariate-specific uncertainties [$\zeta_k^2 = (SE_{k,t} / SD_k)^2$]. Uncertainties for most covariates were included in the models (a few variables, such as presence of *Corbula*, were regarded as fixed). There were sporadic missing data for some covariates, which we allowed to be interpolated within the Markov chain Monte Carlo (MCMC) modeling. These missing covariate values need to be segregated from the main estimation of effects by using the “cut()” function in WinBUGS. If the uncertainties are not so isolated, the model will “sacrifice” fitting precision for the parameters describing dynamics of the response variables to better “fit” missing covariate values, which is not intended (Carrigan et al. 2007).

Priors

Relatively uninformative priors were assigned for these model parameters:

$$\begin{aligned} \gamma_{i,0} &\sim \mathcal{N}(0, 1) & \eta_\gamma &\sim \mathcal{N}(0, 10^3) & \sigma_\gamma &\sim \text{U}(0.01, 10) \\ \sigma_i &\sim \text{U}(0.01, 10) & \delta_{il} &\sim \mathcal{N}(0, 1). \end{aligned} \quad (7)$$

Use of standard Normal priors for the γ_0 and δ parameters is consistent with the expected values being within approximately ± 1 (i.e., constrained to reasonable values) given the ln-transforms for the response variables and the standardized covariates. From expert elicitation, species-specific lags were 2 (delta smelt), 3 (longfin smelt), 5 (striped bass), 2 (threadfin shad), and 1 (calanoids and mysids).

For the key α , β , and γ_1 parameters, we used a Weibull distribution to represent the prior beliefs of the expert-elicited model (Table 2). Use of the Weibull allows long tails in the expected direction if these are supported by the data. We used the construction $\psi_0 \text{Weibull}(2, 1) + \psi_1$, where $\psi_0 = 1$ for expected influences in a positive direction and is -1 for negative expected influences, while ψ_1 is -0.55 for expected influences in a positive direction and 0.55 for negative ones. These configurations invest $\sim 3:1$ prior probability mass in favor of the expected influence. Only one α parameter had a neutral expected influence (Table 2), so this was assigned a $\mathcal{N}(0, 10^3)$ prior (i.e., low precision). Many of the potential relationships were specifically excluded from the model (i.e., deemed unlikely to be

important). For such relationships, coefficients were assigned $\mathcal{N}(0, 10^{-6})$ priors (i.e., 0 with high certainty).

Parameter inference

We inferred importance of model parameters from the probability distributions of the parameters. We computed the proportion of the posterior probability distribution for each parameter exceeding 0 (designated as PPM), which is computed in WinBUGS with the “step()” function. The posterior odds are $\text{PPM} / (1 - \text{PPM})$ for a positive parameter and $(1 - \text{PPM}) / \text{PPM}$ for a negative parameter. The ratio of these posterior odds to the prior odds is termed the odds ratio (OR). Common decision criteria for ORs are 3.2–10 (substantial evidence) and 10–100 (strong evidence) (Jeffreys 1961). For an uninformative prior, in which the ratio of prior probabilities for the parameter is unity, the OR is $\text{PPM} / (1 - \text{PPM})$ (or $(1 - \text{PPM}) / \text{PPM}$ for negative parameters). We used a decision criterion of ≥ 10 for such parameters.

For informative priors, the prior odds were 3 (positive or negative). If the $\text{OR} \geq 3.2$, we concluded that there was substantial support in the data for the expected relationship. If $1 \leq \text{OR} < 3.2$, the data did not invalidate the expectation but there was less support (Jeffreys 1961). If $1 \geq \text{OR} > 1/3.2$, then the data weakly contradicted the expectation. If $\text{OR} \leq 1/3.2$, then the prior ratio of 3:1 had been shifted to 1:1 (or more extreme), suggesting that the expected relationship was inconsistent with the data but likely to be null. We interpreted $\text{OR} < 1/10$ (viz. from 3:1 prior expectation to 1:3.2 posterior odds) as clear refutation of the expected relationship.

Modeling details and model fit

Parameters were estimated from three MCMC chains of 20 000 iterations after 10 000 iterations of burn-in (“model settling”). We checked MCMC mixing and convergence using the “boa” package (Smith 2006) in R (R Development Core Team 2006).

We determined relative importance of the autoregressive (A), among-response variables (R), and covariate (C) factors of the best model. To do so, we calculated the r^2 for eight models: null (fitting constant-only averages for the seven response variables), A, R, C, A + R, A + C, R + C, A + R + C (full model). These models were effected by deleting terms from Eq. 6 as appropriate. The γ_i terms were retained for all models. The r^2 are the squared Pearson correlation coefficients between the z and μ values from the seven response variables and all years. To decompose variance we used hierarchical partitioning (Chevan and Sutherland 1991, Mac Nally 2000), which identifies independent contributions from individual terms (viz. A, R, and C) and joint variance explanation. We used the R package “hier.part” (Walsh and Mac Nally 2003) to perform the decomposition.

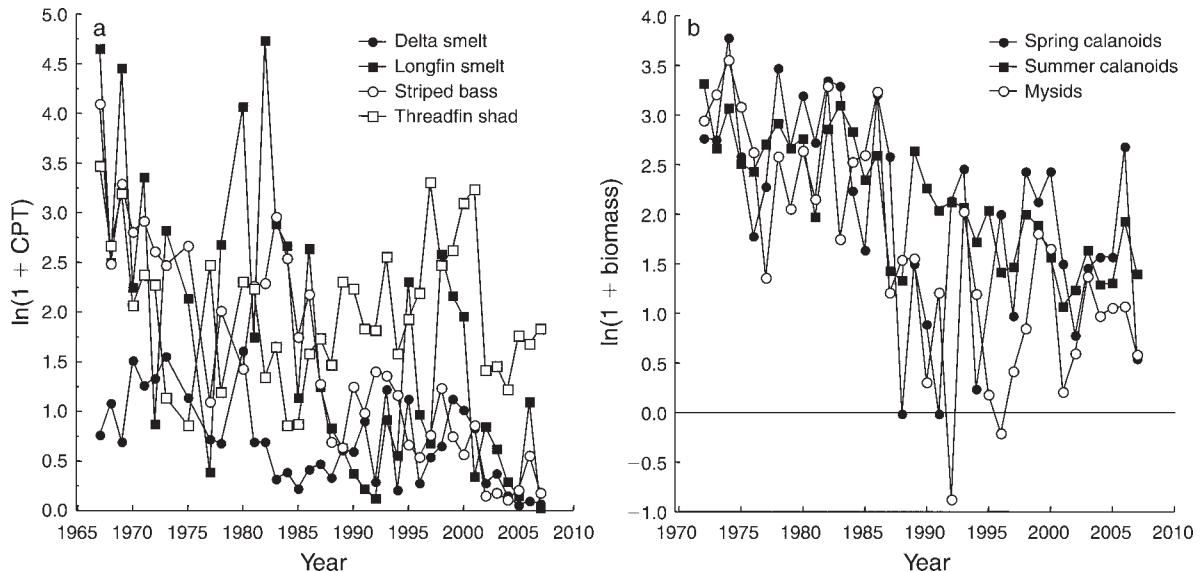


FIG. 2. Population trends (log-transformed) of (a) four fish species (mean catch per trawl [CPT]) and (b) zooplankton taxa (biomass, originally measured in mg C/m^3).

RESULTS

Abundance trajectories

Abundances of all four species of fish declined over the period of data collection, especially since about 2002 (Fig. 2a). Biomasses of the three crustacean groups have been declining consistently since the 1970s, with less evidence of a sudden decline in the 2000s (Fig. 2b).

Overall model characteristics

We used the r^2 (squared Pearson correlation coefficient) between the observed values and the posteriors of the fitted means as our measure of model fit. The full model (autoregressive components, among-response variables interactions, covariates) had an $r^2 = 0.69$. This explained variance was decomposed into independent explanatory amounts of (a) 0.13 for the autoregressive components (A), (b) 0.21 for among-response variable components (R), and (c) 0.35 for covariate relationships (C) (hence 1:1.62:2.69). Thus, the covariates were roughly 66% more important in explaining variation than the response variables, which in turn were ~62% more important than autoregressive elements.

Specific relationships

Parameter estimates and related details are provided in Appendix A. Some covariates appeared to affect more than one response variable (Fig. 3a, b). For expectations that seemed strongly supported by the data, the large values of spring X2 (upstream location) were negatively related to abundances of longfin smelt, biomass of calanoids in spring, and biomass of mysids (Fig. 3a). High water clarity was associated negatively with abundances of striped bass and threadfin shad, while

high mean summer water temperatures had an inverse relationship with delta smelt abundance (Fig. 3a).

Several expectations were more weakly supported by the data, but were not refuted. Spring exports were negatively associated with abundances of delta smelt and threadfin shad (Fig. 3b). Many of the trophic interactions among response variables were supported to some extent, including negative relationships between the abundance of longfin smelt and delta smelt and biomass of calanoids in summer, negative correlations between abundance of striped bass and calanoid biomass in spring, and a positive relationship between concentration of chlorophyll *a* in spring and biomass of mysids and calanoids. Calanoid biomass in spring and summer was negatively associated with presence of the nonnative clam *Corbula amurensis*, while abundance of largemouth bass and volume of winter exports were negatively associated with abundance of delta smelt (Fig. 3b).

For all four declining fish species, the parameters indicating density dependence (δ) from the previous year were strongly negative, ranging from -0.79 ± 0.26 (mean \pm SD) for threadfin shad to -1.03 ± 0.18 for longfin smelt (Appendix A). Current abundances were positively related to those for two years previous for longfin smelt (0.30 ± 0.16). Other lag effects were deemed unimportant, although a four-year lag (positive) for striped bass had OR = 9.2.

For the γ parameters, only one result seemed unexpected. The anticipated negative slope for threadfin shad was positive, with high certainty (OR < 1/57.8; Appendix A). This suggested, counterintuitively, that the intrinsic population growth parameter had increased over the duration of study.

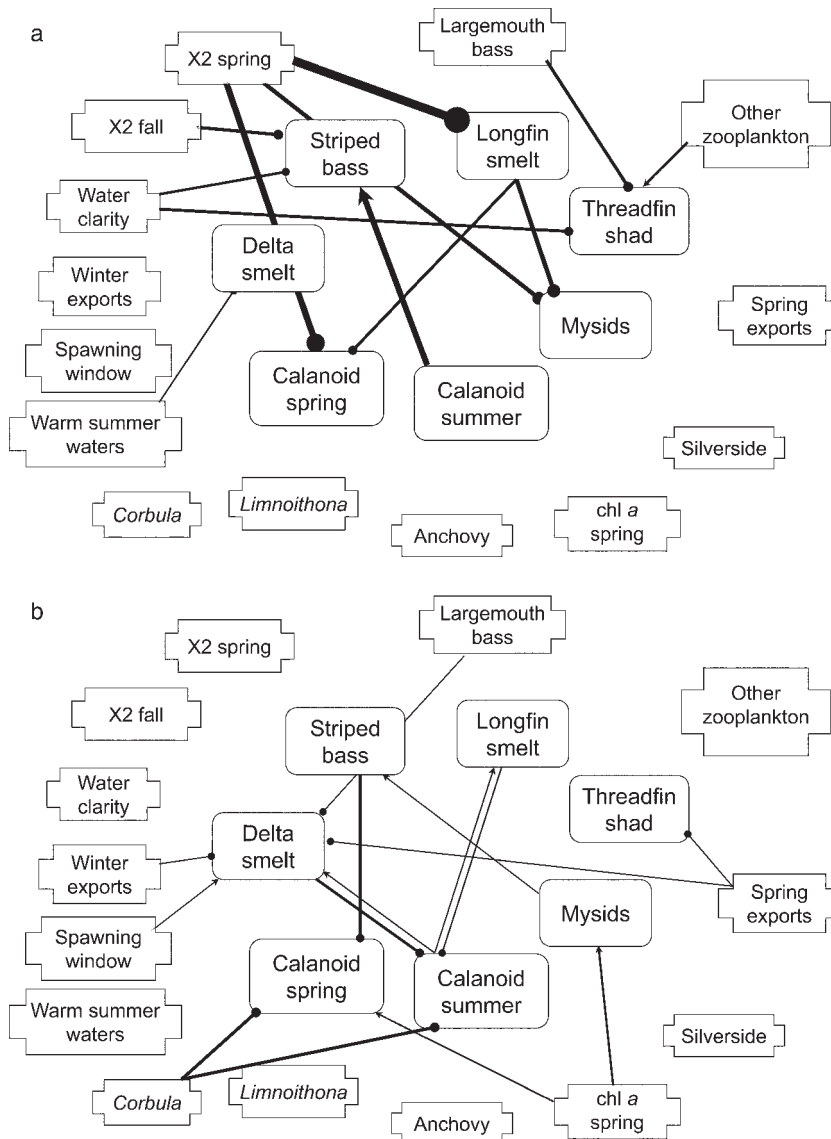


FIG. 3. Relationships supported by the Bayesian multivariate autoregressive analysis of the expert-elicited model, with width of lines proportional to the regression coefficient divided by its standard error. Response variables (focal taxa) are enclosed in rounded boxes while covariates are in boxes with side tabs. Arrows toward a focal taxon indicate a positive effect related to the focal taxon or covariate of line origin, while solid circles indicate negative relationships. (a) Relationships for which the odds ratio ≥ 3.2 . (b) Relationships for which the odds ratio falls between 1 and 3.2. The abbreviation “X2” refers to the 2‰ isohaline.

DISCUSSION

Overview of the MAR results

The importance of covariates (51% of explained variation) suggests that some aspects of the environment that can be managed are associated with the declining fish species (e.g., X2 and exports). However, other potential remedial actions would be difficult or impossible to enact (e.g., total removal of *Corbula amurensis*). The relatively large proportion of variance explained by interactions among the declining fishes and their prey suggests that trophic interactions also are important, but

it is less clear how management actions could modify such relationships.

The MAR analysis largely supported the expert model, suggesting that existing knowledge is sufficient to identify important interactions and processes, although not all relationships were supported. The expert model included 54 relationships, all but one of which was assigned an expected direction (Table 2). The latter was an “uninformed” expectation that calanoids in spring would be affected by spring X2. The direction was found to be strongly negative (Fig. 3a), suggesting that spring calanoid abundance is greater when X2 is

more seaward. Of the 53 relationships with expected directions, 13 were strongly supported on the basis of odds ratios (OR) of ≥ 3.2 (Fig. 3a) and 15 were not inconsistent with the expected direction ($3.2 > \text{OR} \geq 1$) (Fig. 3b). The other 25 coefficients had posterior means close to zero, indicating that the data did not support the expected directions.

One advantage of using the MAR approach is that results can be represented easily in a form with which most ecologists are familiar, a (partial) food web (Fig. 3). The predator–prey relationships involving the calanoids and mysids support existing reports of direct and indirect effects on the four declining fish species. For example, abundance of striped bass was positively related to availability of calanoid copepods in summer (Fig. 3a). This was negatively associated with the occurrence of the introduced clam *Corbula amurensis* (Fig. 3b), which has induced an ongoing decrease of $\sim 60\%$ in chlorophyll *a* concentration in the low-salinity zone (Alpine and Cloern 1992). Other indirect food limitation relationships may be the chlorophyll *a* (spring) \rightarrow mysids \rightarrow striped bass and chlorophyll *a* (spring) \rightarrow calanoids (spring) \rightarrow striped bass pathways (Fig. 3b). Longfin smelt abundances had strong negative correlations with calanoids in spring and summer and mysids in spring (Fig. 3a, b). Abundance of delta smelt was related to calanoid biomass in summer (Fig. 3b). These results and relationships of copepods and mysids to chlorophyll *a* concentrations (Fig. 3b) suggest that food web dynamics are important for both smelt species. The isohaline position (X2) in spring had strong negative relationships with spring calanoids and mysids, which also would propagate back through those food pathways (Fig. 3a).

Few covariate relationships were expressed clearly for more than one of the four declining fish species (Fig. 3a, b). Increased water clarity appeared to be related negatively to both striped bass and to threadfin shad (Fig. 3a). Increased water clarity has been attributed to reduction of sediment supply in the rivers (Wright and Schoellhamer 2004) and to sediment capture by submerged aquatic vegetation. Water clarity affects fish feeding (Hecht and Vanderlingen 1992) and vulnerability to predation (Gregory and Levings 1998). Abundance of largemouth bass, a potential predator of the declining fish species (Nobriga and Feyrer 2008), was negatively related to abundance of threadfin shad and, more weakly, to abundance of delta smelt (Fig. 3). Abundance of largemouth bass has increased in the Delta concurrently with expansion of submerged aquatic vegetation (Brown and Michniuk 2007), which provides high-quality habitat for the species. Greater cover of submerged aquatic vegetation also reduces turbidity. Reduced water clarity has been identified as a key component of habitat for delta smelt, at least in autumn (Feyrer et al. 2007). The absence of a discernible relationship between water clarity and abundance of delta smelt may be due to an indirect expression through

trophic relationships. Young delta smelt require suspended particles in the water column to feed properly (Baskerville-Bridges et al. 2002, Mager et al. 2002), so reduced prey availability (e.g., summer calanoids) may mask the direct water clarity effect. The multiple effects of temperature, feeding, exports, and introduced species are more consistent with understanding of delta smelt biology (Bennett 2005, Baxter et al. 2008) than are effects of individual covariates per se.

There were clear relationships between warmer summer waters (negative) and duration of water temperatures suitable for spawning (positive) (Fig. 3) and delta smelt, which were consistent with known effects of high temperatures on delta smelt survival (Swanson et al. 2000) and spawning requirements (Bennett 2005).

Increases in water exports in both winter and spring were negatively associated with abundance of delta smelt and increases in spring exports with abundance of threadfin shad. Losses of delta smelt previously have been related to exports through entrainment and mortality at pumping facilities and may be important to population dynamics under some circumstances, particularly during dry years (Kimmerer 2008). Effects of spring exports on threadfin shad have not been measured but possibly are important given that this is the only species of the four to occupy freshwater throughout its life cycle and whose main distribution is near the export facilities (Feyrer et al. 2009).

Modeling formulation: data and limitations

Using MAR, we identified plausible results, notwithstanding a number of important caveats within the model framework, which relate to the nature of the underlying data and to the structure of the analytical model.

Data limitations.—Three major forms of data limitation inherent in MAR are relevant to our study: (1) characterization of all variables and covariates by using a single value per year; (2) lack of spatially and temporally explicit data; and (3) selection of covariates and their measurement. For the declining fish species, we used an estimate of abundance based on average catch per sampling trawl over ~ 100 sampling stations over each of the four autumn months (September to December). Fish have been collected by other sampling methods (e.g., beach seine nets), but either not consistently over the duration of the data collection or only recently. We included observation error as the standard error from the ~ 400 trawls per year, but whether this is the most appropriate measure is arguable (Newman 2008).

Apart from allowing γ_t to be time-dependent (albeit linearly), the MAR model assumed process stationarity over the entire duration, which means that the structure of the model and distributions of model parameters are regarded as being the same over the 40+ years. It is possible that population dynamics of the declining taxa

changed greatly as a function of population size. It is plausible that per capita reproductive rates, age structures, social (e.g., schooling) behaviors, Allee effects (Stephens and Sutherland 1999), and vulnerability to predation may differ when there are many individuals compared to when there are few. This is a common tenet in conservation biology (Caughley 1994).

Given the high certainty that all four species declined in concert in 2002 (Thomson et al. 2010), we modified Eq. 6 to allow all parameters to have a two-phase structure. The first phase was the 1967–2001 period and the second phase was 2002–2007. Each parameter was represented by a term of the form $\alpha + \delta\alpha$, where $\delta\alpha$ was the deviation in the second phase from values in the first phase. There were no parameters in which $\delta\alpha$ differed substantially from zero using our OR criteria. This suggests that the stationarity assumption of the MAR model is reasonable, although the small number of years in phase two may make changes difficult to detect.

Stakeholders have commissioned extensive correlative analyses (D. Fullerton, W. J. Miller, and B. F. J. Manly, *unpublished data*), which suggest a wide range of possibilities for potential covariates that might have sparked the precipitous declines. We included eight commonly mentioned covariates in additional runs of the MAR model (Appendix B). Our inferences were little changed, which suggests that our expert model was resilient to inclusion of additional variables and that the latter were largely uninformative.

Model form and structure.—The MAR model is underlain by the Gompertz population dynamic model (Eq. 1). Inference on stock recruitment is contingent on the form of the model (Maunder 2003). We explored whether our inferences were highly dependent on the use of the Gompertz by replacing it with another widely used formulation, the Ricker model (Appendix C; Zeng et al. 1998). The Ricker model emphasized more strongly several relationships: for example, the negative relationships between striped bass and X2 (autumn) and between spring calanoids and X2 (spring) (Appendix C). The Ricker and Gompertz versions of the MAR model generally provided similar inferences but the Gompertz appeared to resolve with greater precision a larger number of relationships given our criteria for their identification (i.e., using ORs).

The values for the δ_{i1} coefficients for the four declining fish species suggested strong negative density dependence (values between -0.79 and -1.03 for one-year lag; Appendix A). Such results seem difficult to reconcile biologically given that the fish sampled each year are young-of-the-year and it is difficult to conceive of a mechanism producing such density dependence. It is possible that this apparent contradiction may be a statistical artifact of the parameterization of the usual Gompertz model. Estimates of γ and δ can be highly correlated and identifiability depends upon length of time series (J. Ponciano, *personal communication*). Even

if there were estimation problems for γ and δ , these probably do not affect our estimates of trophic interactions and covariate relationships. From simulations of a Gompertz model with one covariate, we found that the estimate for the covariate coefficient was unbiased even though the estimates of γ and δ were biased (results not shown).

The MAR formulation assumed linear relationships (on the log-abundance scale) and no interactions among covariates, although many interactions are plausible. Interactions would add substantially to the complexity and difficulty of interpretation of an already highly parameterized model. Inclusion of nonlinear functions and interactions among covariates may reduce capacity to resolve drivers of responses if used injudiciously.

A comparison of major outcomes of the MAR analysis with those of the change point analyses, which did allow nonlinear functions of covariates, showed some commonalities, but also several differences. Relationships with water clarity were important in the change point analyses for delta smelt, striped bass, and longfin smelt, although the relationship for the latter was rather stronger in a multispecies model (Thomson et al. 2010). A correlation of water clarity with abundances of threadfin shad, but not with delta smelt, was identified in MAR. A pervasive relationship of spring X2 with abundances of longfin smelt was clear in both analyses. A correlation of winter exports with delta smelt was evident in the change point, but was weaker in the MAR (Fig. 3b). The MAR analysis, but not the change point analysis, identified a correlation between autumn X2 and striped bass. Spring exports appeared to be related to abundances of threadfin shad in both analyses, although the magnitude of the correlation was less in the MAR. Unlike the change-point analysis, the MAR analysis did not identify a relationship between winter exports and threadfin shad. However, in the change-point analysis the magnitude of the average regression coefficient for winter exports and threadfin shad was substantially less than that for spring exports (Thomson et al. 2010). The trophic interactions evident in the MAR, of which many were pronounced (Fig. 3), were less evident in the model selection procedures used in the change point analysis.

A broader life-history model with a more general state-space approach to modeling the pelagic species decline should be more informative (M. N. Maunder and K. B. Newman, *personal communication*). Such a model would incorporate multiple sources of survey data, including data pertinent to egg, larval, juvenile, and adult phases and covariates appropriate for each stage (Maunder 2004).

Estuarine management

Our application of the MAR model provides evidence from a multivariate analysis of how abiotic habitat factors directly relate to declining fish abundance in the upper San Francisco Estuary and indirectly to these fish

populations through the food web. Synthesis of previous univariate analyses have come to similar conclusions, albeit indirectly (Bennett 2005, Baxter et al. 2008). Before the fish species declined precipitously, the abiotic component of their habitat in the estuary was represented mainly as X2 because position of the salinity field was correlated with the abundances of many organisms (Jassby et al. 1995). Recent results have highlighted the importance of other abiotic variables, including water clarity and water temperatures, in the estuary (Feyrer et al. 2007, Nobriga and Feyrer 2008). Our results, which identify trophic relationships, suggest the need to better understand the processes underlying the influence of abiotic conditions on the food web of the estuary. The upper San Francisco Estuary is an exemplar, perhaps an extreme one, of severe, adverse ecological response to many of the stressors to which such systems increasingly are exposed (Fig. 3). Some of the key issues relate to how the isohaline position (X2), which seems to have a profound effect on the declining fish and on their prey, might be managed. While evidence that water exports directly affect striped bass or longfin smelt in a consistent linear manner is weak, there is evidence of potential effects of water exports on delta smelt and threadfin shad. Successfully managing the estuary, at least for the declining fish species, requires a more complete understanding of how the direct effects of water exports interact with the indirect effect of controlling abiotic conditions and the food web.

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APPENDIX A

Details of parameter estimates for the multivariate autoregressive (MAR) model including credible intervals of odds ratios (all model parameters are listed) (*Ecological Archives* A020-050-A1).

APPENDIX B

Details of parameter estimates for multivariate autoregressive (MAR) model with and without distinct variables suggested by other analyses (only parameters with large odds ratios are listed) (*Ecological Archives* A020-050-A2).

APPENDIX C

Details of parameter estimates for multivariate autoregressive (MAR) models underlain by Ricker and Gompertz population-dynamic formulations (only parameters with large odds ratios are listed) (*Ecological Archives* A020-050-A3).