Explaining Patterns of Pelagic Fish Abundance in the Sacramento-San Joaquin Delta

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Explaining Patterns of Pelagic Fish Abundance in the Sacramento-San Joaquin Delta

Robert J. Latour[1]

Abstract Investigating the effects of environmental, biological, and anthropogenic covariates on fish populations can aid interpretation of abundance and distribution patterns, contribute to understanding ecosystem functioning, and assist with management. Studies have documented declines in survey catch per unit effort (CPUE) of several fishes in the Sacramento-San Joaquin Delta, a highly altered estuary on the US west coast. This paper extends previous research by applying statistical models to 45 years (1967–2012) of trawl survey data to quantify the effects of covariates measured at different temporal scales on the CPUE of four species (delta smelt, *Hypomesus transpacificus*; longfin smelt, *Spirinchus thaleichthys*; age-0 striped bass, *Morone saxatilis*; and threadfin shad, *Dorosoma petenense*). Model comparisons showed that along with year, the covariates month, region, and Secchi depth measured synoptically with sampling were all statistically important, particularly in explaining patterns in zero observations. Secchi depth and predicted CPUE were inversely related for all species indicating that water clarity mediates CPUE. Model comparisons when the year covariate was replaced with annualized biotic and abiotic covariates indicated total suspended solids (TSS) best explained CPUE trends for all species, which extends the importance of water clarity on CPUE to an annual timescale. Comparatively, there was no empirical support for any other annualized covariates, which included metrics of prey abundance, other water quality parameters, and water flow. Top-down and bottom-up forcing remain important issues for understanding delta ecosystem functioning; however, the results of this study raise new questions about the effects of changing survey catchability in explaining patterns in pelagic fish CPUE.

Keywords Delta and longfin smelt · Sacramento-San Joaquin Delta · Zero-inflated generalized linear models · Water flow · Zooplankton · Water quality

Introduction

The dynamics of fish populations involve a complex suite of biological processes operating at different temporal and spatial scales. Abiotic and biotic variables modulate the intrinsic biological properties of individual fish species and structure the diversity and abundances of species within ecosystems. Such variables can be ecological, environmental, climatic, and anthropogenic, and they synthetically influence ecosystem dynamics. Ecological variables are often described in the context of bottom-up (Chavez et al. 2003; Frederiksen et al. 2006) or top-down (Cury and Shannon 2004; Hunt and McKinnell 2006) control of food webs, while environmental variables such as temperature, dissolved oxygen, and others have been shown to influence early life history (Norcross and Austin 1988) and the distribution of fishes within ecosystems (Breitburg 2002; Craig 2012; Buchheister et al. 2013). Climate variability can have a multipronged impact, exerting influence on specific life stages, such as the formation of new year classes (Houde 2009), or at the level of individual species (Hare et al. 2010) or whole ecosystems (Winder and Schindler 2004; Drinkwater et al. 2009). Numerous anthropogenic stressors such as pollution, nutrient enrichment and eutrophication, introduction of nonnative species, and perhaps most notably, overexploitation have been documented to influence

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ecosystem structure and fish abundance (Islam and Tanaka 2004; Molnar et al. 2008; Diaz and Rosenberg 2008; Worm et al. 2009).

Globally, centuries of anthropogenic change have transformed estuarine and coastal waters into systems with reduced biodiversity and ecological resilience (Jackson et al. 2001; Lotze et al. 2006). Given the importance of these areas to marine life, efforts to remediate the cascading effects of anthropogenic stressors will undoubtedly require deep consideration of principles inherent to ecosystem-based management (EBM; Link 2010). However, before strategic and tactical management policies can be effectively implemented, EBM rooted or otherwise, the relative roles of natural and anthropogenic factors that affect ecosystem structure and associated species abundances must be well understood.

San Francisco Bay is a tectonically created estuary located on the US Pacific coast that has experienced considerable anthropogenic change (Nichols et al. 1986). The bay and its watershed occupies 1.63×10^7 ha and drains 40 % of California's land area (Jassby and Cloern 2000). Freshwater is supplied to the estuary primarily from the Sacramento and San Joaquin rivers, which converge to form a complex mosaic of tidal freshwater areas known collectively as the Sacramento-San Joaquin Delta (referred herein as the delta). Most naturally occurring wetlands in the estuary have been lost due to morphological changes to the system for agriculture, flood control, navigation, and water reclamation activities (Atwater et al. 1979). Other notable changes include modifications to the volume of freshwater entering the delta and thus the natural delivery of land-based sediment (Arthur et al. 1996), massive sediment loading resulting from large-scale hydraulic mining activities (Schoellhamer 2011), introduction and invasion of nonindigenous species (Cohen and Carlton 1998), input of contaminants (Connor et al. 2007), and reported decreases in chlorophyll-a (Alpine and Cloern 1992), zooplankton (Orsi and Mecum 1996), and fish catch per unit effort (CPUE; Sommer et al. 2007).

A variety of tools can be used to understand how specific changes to ecosystem components influence fish population dynamics. These include directed field studies, statistical analyses, and multidimensional mechanistic modeling activities, with all often being required to develop a robust understanding of ecosystem dynamics. In the delta, there has been a considerable focus on empirical analyses designed to examine how temporal trends in CPUE statistically relate to various abiotic and biotic variables. Researchers have described freshwater flow within the delta as a key structuring variable of fish CPUE (Turner and Chadwick 1972; Stevens and Miller 1983; Sommer et al. 2007) along with the salinity variable X_2, which is defined as the horizontal distance up the axis of the estuary where the tidally averaged near-bottom salinity is 2 psu (Jassby et al. 1995; Kimmerer 2002; Kimmerer et al. 2009; MacNally et al. 2010). However, the evidence supporting

these inferences was based on relationships between annual CPUE indices and metrics of water flow and/or X_2, which can be limiting since collapsing many raw field observations of CPUE into annual indices leads to a sizable loss of potentially valuable information. Feyrer et al. (2007, 2011) applied statistical models to raw survey data collected from the delta to quantify fish occurrences in relation to water quality variables; however, they did not examine CPUE or consider variables at broader temporal scales.

This study builds on previous empirical analyses by examining how measures of CPUE in the delta statistically relate to a broad suite of abiotic and biotic variables across multiple temporal scales and exclusively from the perspective of raw field observations. The analyses presented here follow a two-step procedure that reflects the specific objectives of this study, (1) investigate the role of covariates measured synoptically at the time of fish sampling to elucidate their effects on CPUE and (2) modify the analytical framework used for the first objective to examine the relative role of various abiotic and biotic covariates hypothesized to influence CPUE at an annual timescale. For the second objective, the covariates considered were annualized metrics of zooplankton density, chl-a concentration, water quality, and water flow. These analyses contribute to the understanding of ecosystem dynamics within the delta and thus aid the formulation of EBM strategies by providing foundational information of fish population responses to natural and anthropogenically modified system attributes.

Methods

Focal Fish Species

Reported declines of fish CPUE in the delta have revolved primarily around four species: delta smelt, *Hypomesus transpacificus*, longfin smelt, *Spirinchus thaleichthys*, age-0 striped bass, *Morone saxatilis*, and threadfin shad, *Dorosoma petenense*. Accordingly, these species are the focus this study. The delta smelt is a relatively small (60–70 mm standard length (SL)), endemic, annual, spring spawning, planktivorous fish that is distributed primarily in the delta and surrounding areas (Moyle et al. 1992). Delta smelt were listed as threatened under the US Endangered Species Act (ESA) in 1993 and endangered under the California Endangered Species Act (CESA) in 2010. The endemic longfin smelt is also a relatively small (90–100 mm SL), anadromous, semelparous, spring spawning fish with an approximate 2-year life cycle that is broadly distributed throughout the estuary (Rosenfield and Baxter 2007). Longfin smelt were listed as threatened under the CESA in 2010. Striped bass is a larger (>1 m SL), relatively long-lived, anadromous, late-spring spawning species deliberately introduced to the San

Francisco Estuary from the US east coast in 1879 (Stevens et al. 1985). Although subadult and adult fish reside primarily in estuarine and coastal waters, age-0 fish can be found in lower salinity areas where they feed on zooplankton and macroinvertebrates. Threadfin shad was discovered in the delta during the early 1960s (Feyrer et al. 2009) and is a relative small (<100 mm SL), summer spawning planktivorous fish that primarily inhabits freshwater areas of the estuary.

Field Sampling

The California Department of Fish and Wildlife (CDFW) has been conducting the Fall Midwater Trawl (FMWT) survey in the delta nearly continuously since 1967 (Stevens and Miller 1983; see http://www.dfg.ca.gov/delta/projects.asp? ProjectID=FMWT for additional details). The survey was initiated to measure the relative abundance of age-0 striped bass; however, survey data have been used to infer patterns in relative abundance of a variety of species inhabiting the delta (Kimmerer 2002; Sommer et al. 2007). Monthly cruises are conducted from September through December, and the number of tows each month has increased from approximately 75–80 during the early years of the program to >100 in more recent years. The survey follows a stratified fixed station design such that sampling occurs at approximately the same location within predefined regional strata (17 areas excluding areas 2, 6, and 9 per the CDFW's protocol). Sampling intensity is related to water volume in each regional stratum such that samples are taken every 10,000 acre ft for areas 1–11 and every 20,000 acre ft for areas 12–17; Fig. 1). At each sampling location, a 12-min oblique tow is made from near bottom to the surface using a 3.7 m×3.7 m square midwater trawl with variable mesh in the body and a 1.3-cm stretch mesh cod end. Vessel speed over ground during tows can be variable since sampling procedures are designed to maintain a constant cable angle throughout the tow. Each catch is sorted and enumerated by species and station-specific measurements of surface water temperature, electrical conductivity (specific conductance), and Secchi depth are recorded. CPUE is defined as number of fish collected per trawl tow.

Sampling Covariates

Generalized linear models (GLMs; McCullagh and Nelder 1989) were used to evaluate the effects of sampling covariates on CPUE of the four focal fish species. GLMs are defined by the underlying statistical distribution for the response variable and how a set of linearly related explanatory variables correspond to the expected value of the response variable. The relationship between explanatory variables and the expected value of the response variable is defined by a link function, which must be differentiable and monotonic.

Since CPUE was defined as fish count per trawl, the Poisson and negative binomial distributions were considered. Plots of the proportion of FMWT tows where at least one target animal was captured across the time series for each species showed low values for many years, which gave rise to the possibility that these data were zero-inflated (Fig. 2). In general, zero-inflated count data imply that the response variable contains a higher proportion of zero observations than expected based on a Poisson or negative binomial count process. Ignoring zero inflation can lead to overdispersion and biased parameter and standard error estimates (Zuur et al. 2009).

Zero-inflated distributions are a mixture of two distributions, one that can only generate zero counts and another that includes zeros and positive counts. In effect, the data are divided into two groups, where the first group contains only zeros (termed false zeros) and the second group contains the count data which may include zeros (true zeros) along with positive values (Zuur et al. 2009, 2012). To identify the appropriate model structure (zero-inflated versus standard GLM) and distribution of the count data (negative binomial versus Poisson), a variety of preliminary models were fitted to the FMWT data. Diagnostic plots, evaluation of overdispersion, and model comparisons using likelihood ratio tests and Akaike's information criterion (AIC; Akaike 1973; Burnham and Anderson 2002) all strongly supported application of a zero-inflated negative binomial distribution, which can be expressed as (Brodziak and Walsh 2013):

$$\Pr(y_i) = \begin{cases} \pi_i + (1-\pi_i) \cdot \left(\dfrac{k}{\mu_i + k}\right)^k & y_i = 0 \\[2ex] (1-\pi_i) \cdot \dfrac{\Gamma(y_i + k)}{\Gamma(k) \cdot \Gamma(y_i + 1)} \cdot \left(\dfrac{k}{\mu_i + k}\right)^k \cdot \left(\dfrac{\mu_i}{\mu_i + k}\right)^{y_i} & \text{otherwise} \end{cases}$$

$$(1)$$

where y_i is the ith CPUE observation, π_i is the probability of a false zero, and μ_i and k are the mean and overdispersion parameters of the negative binomial distribution, respectively. The top equation represents the probability of obtaining a zero CPUE value, which is a binomial process that can occur either as a false zero or a true zero adjusted by the probability of not obtaining a false zero. The bottom equation is the familiar negative binomial mass function adjusted by the probability of not obtaining a false zero. GLMs were specified to mode π_i and μ_i as linear combinations of covariates with logit and log link functions, respectively.

The covariates measured synoptically with sampling that were considered included year, month, area (all categorical), and the continuous covariate Secchi depth, which was rescaled by subtracting the mean and dividing by its standard deviation. Inclusion of levels of categorical covariates with very few positive CPUE values caused model convergence and estimation problems, so levels with <5 % of the total
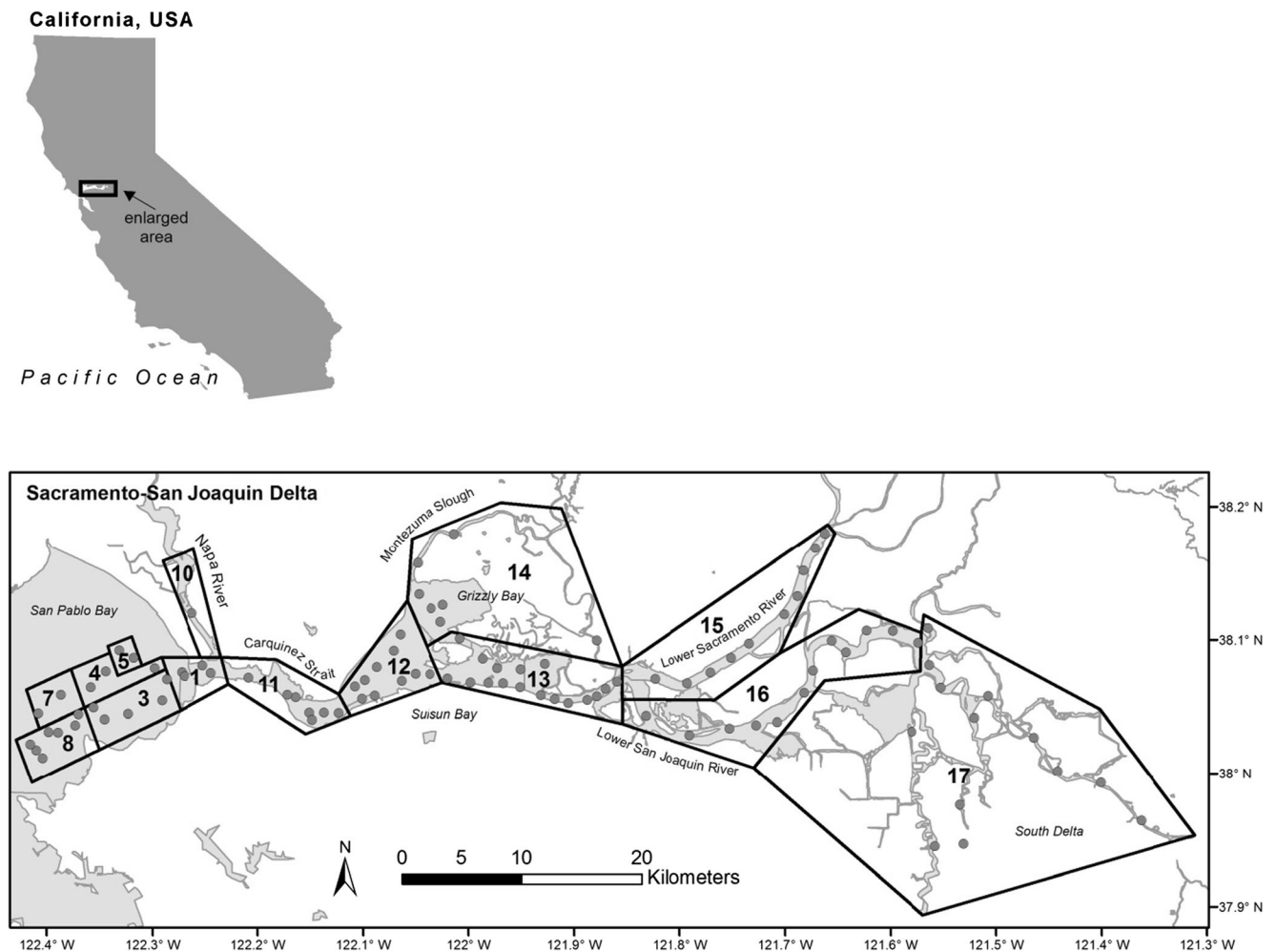
Fig. 1 Aerial stratification (*polygons*) and sampling locations (*circles*) for the Fall Midwater Trawl survey within the Sacramento-San Joaquin Delta, 1967–2012. Areas 2, 6, and 9 are not shown because they have not been consistently sampled and thus are not used by the California Department of Fish and Wildlife for estimation of catch per unit effort indices. No sampling occurred in 1974, September 1976, December 1976, and 1979. Figure adapted from Newman (2008)

survey catch of each species were deemed uninformative and excluded from the analysis. The covariates surface water temperature and surface salinity were also considered; however, variance inflation factors indicated that month/temperature and area/salinity were collinear. Month and area were chosen over temperature and salinity because an appreciable number of catch records did not have associated measures of temperature and/or salinity, and it was desirable to base analyses on the most available information. Also, the variables month and area arguably have the potential to be more useful in a management context. Interaction terms were excluded because the high proportion of zeros in the data lead to many year/area and month/area combinations for which there were no positive CPUE observations. Model parameterizations for each species ranged from inclusion of only a year covariate for the count and probability of false zero models to the saturated model with all four covariates specified for both components, including the possible combinations of unbalanced covariate specifications. AIC was used for model selection, and predictions

were generated from the most supported model using estimated marginal means (Searle et al. 1980). Coefficients of variation for yearly predicted CPUE values were estimated from standard deviations of 1000 nonparametric bootstrapped samples (Efron and Tibshirani 1993). Models were fitted to data from 1967 to 2012 with the exception of 1974, September 1976, December 1976, and 1979 when no sampling occurred.

Annual Covariates

The covariate year is included in models when the goal is to develop a time series of estimated CPUE indices. However, the year covariate is simply a proxy for the ecosystem conditions over an annual timescale and thus has no direct relation to the vital rates of fish populations. Therefore, to more directly investigate factors potentially underlying interannual patterns in CPUE for each fish species, the aforementioned zero-inflated GLM structure was modified in two ways: (1) the year covariate was replaced by several hypothesized biotic and abiotic
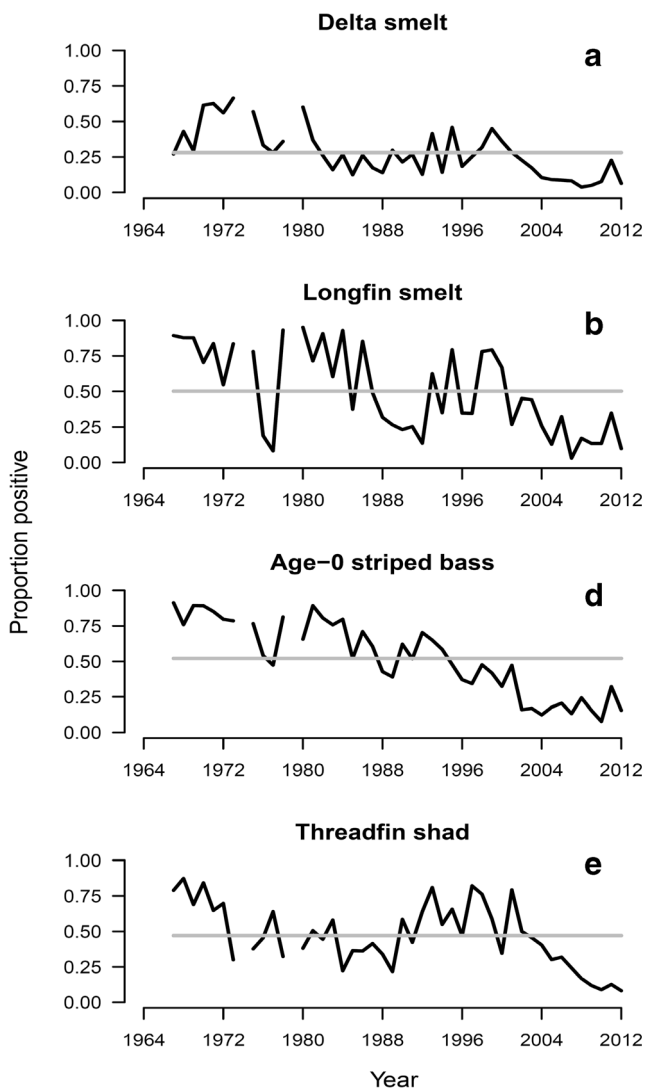
Fig. 2 Yearly proportions of positive tows (at least one target animal captured) based on the Fall Midwater Trawl survey, 1967–2012, for **a** delta smelt, **b** longfin smelt, **c** age-0 striped bass, and **d** threadfin shad. No sampling occurred in 1974, September 1976, December 1976, and 1979. *Horizontal line* is the time series mean

annualized continuous covariates, which operationally implied that the yearly value of each annualized covariate was assigned to each observed CPUE corresponding to the same year and (2) a single parameterization that included the annualized covariate along with month and area was fitted to isolate the effect of each annualized covariate on CPUE. Broad categories of the annualized covariates were zooplankton density (several taxa), chl-*a* concentration as a proxy for phytoplankton biomass, water quality metrics, and water flow (a total of 26). The years analyzed were 1976–2010, which was due to availability of chl-*a* data (began in 1976) and water flow measures (obtained through 2010). AIC was used to compare among competing annualized covariates for each fish species.

In terms of biotic covariates, the California Department of Water Resources (DWR) in collaboration with the CDFW

have been compiling data on zooplankton density in the delta since 1968 (see http://www.water.ca.gov/bdma/meta/zooplankton.cfm for additional details, including specific sampling locations). The zooplankton monitoring program was initiated to investigate the population trends of pelagic organisms consumed by young fishes, particularly age-0 striped bass. Although the initial focus was to evaluate seasonal patterns in mysid abundance, the program expanded shortly after its inception to assess population levels of other key zooplankton taxa. Sampling occurs monthly at approximately 20 fixed stations. The zooplankton sampling gear consists of a Clarke-Bumpus net mounted directly above a mysid net, and the unit is deployed in an oblique fashion from near bottom to the surface. Each net is equipped with a flow meter, and all samples are preserved for sorting in the laboratory. For each station, zooplankton taxa are expressed as the total number per cubic meter of water sampled. Starting in 1976, chl-*a* concentration was recorded synoptically with zooplankton sampling.

The zooplankton taxa examined were adult calanoid copepods, adult cyclopoids, a combination of the two, and mysids. Annual estimated mean densities of zooplankton and chl-*a* were based on lognormal GLMs fitted to data from the core sampling locations and first replicate sample. The categorical covariates considered were year, survey (which is approximately equivalent to month), and area along with the continuous variable Secchi depth, which was again rescaled. Levels of categorical variables with <5 % of the total zooplankton density of each group again caused estimation problems and excluded from the analysis. Collinearity was assessed using variance inflation factors, and bias-corrected predicted (Lo et al. 1992) time series were generated from the most supported model using estimated marginal means.

In terms of abiotic covariates, the DWR has been monitoring water quality parameters at discrete sampling locations in the delta since 1970 (see http://www.water.ca.gov/bdma/meta/discrete.cfm for additional details, including sampling locations). The program was established to provide information for compliance with flow-related water quality standards for the delta set forth in the series of regulatory water right decisions and to provide abiotic data that could aid the interpretation of results from concurrent biological monitoring programs. Samples are taken at approximately 1 m depth and roughly within a 1-h window of the expected occurrence of high tide from 19 fixed stations. Sampling frequency is bimonthly during the rainy season (October/November to February/March) and monthly during the dry season (March/April to September/October).

Annual water quality metrics considered were mean summer (Jul–Sep) and winter (Jan–Mar) water temperature, total suspended solids (TSS) or filterable solids, volatile suspended solids (VSS) as a measure of the organic component of TSS, and turbidity. The annual mean water temperatures were

estimated from a multiple linear regression model while annual mean TSS, VSS, and turbidity estimates were obtained from bias-corrected lognormal GLMs. The covariates considered were categorically defined year, month, and area. Variance inflation factors were again used to assess collinearity, and predicted mean values for each year were based on estimated marginal means from the most supported model.

The water flow covariates considered were classified into two groups, "historical", which refers to measured flows taken from monitoring equipment located at various points in the delta, and "unimpaired", which is an estimated reference quantity intended to represent broader watershed-level hydrology in the absence of man-made facilities that affect flow. For each group, monthly inflow and outflow time series were assembled. Historical inflow included combined measurements from the Sacramento River, Yolo Bypass, and Eastern Delta (San Joaquin River and adjacent areas; Fig. 1), while historical outflow is a net quantity of inflow and an estimate of delta precipitation less total delta exports and diversions. All historical flow time series were based on DAYFLOW, which is a computer program designed to estimate daily average delta outflow (see http://www.water.ca.gov/dayflow/ for more details). Unimpaired inflow is an estimate of water entering the delta from the expansive watershed while unimpaired outflow is a net value adjusted for natural losses (e.g., evaporation and vegetation uptake). Flow data were provided courtesy of W. Bourez (MBK Engineers, Sacramento, CA).

For each flow covariate, a single value was calculated by averaging monthly flow values in four different ways: (i) from Jan–Jun within the year of sampling, (ii) from Mar–May within the year of sampling, (iii) from Jan–Jun of the preceding sampling year, and (iv) from Mar–May of the preceding sampling year. This approach gave rise to 16 annual flow covariates. Lagged flow covariates were considered to investigate possible delayed effects of flow on CPUE. For the most supported annualized covariate, 95 % prediction intervals of CPUE and probabilities of false zeros were based on 1000 nonparametric bootstrapped model fits (Efron and Tibshirani 1993). All statistical analyses were performed with the software package R (version 2.15.1, R Development Core Team 2012), and zero-inflated GLMs were fitted by accessing the "pscl" library.

Results

Field Sampling

Complete tow, month, area, and Secchi depth information was available for 15,273 stations sampled during monthly fall cruises from 1967 to 2012 (excluding 1974, Sep 1976, Dec 1976, and 1979 when no sampling occurred).

Application of the 5 % cutoff rule for levels of categorical covariates indicated that all levels of month contained adequate nonzero CPUEs for inclusion in analyses. However, spatial data summaries showed that CPUEs were quite low in some areas, and the 5 % rule led to the inclusion of only areas 12–16 for delta smelt, 11–14 for longfin smelt, 12–16 for YOY striped bass, and 15–17 for threadfin shad (Fig. 1). Total numbers of tows analyzed for each species were 8802 for delta smelt (max. CPUE of 156 animals in December 1982), 6582 for longfin smelt (max. CPUE of 3358 animals in September 1969), 8733 for age-0 striped bass (max. CPUE of 1100 animals in September 1967), and 5019 for threadfin shad (max. CPUE of 4012 animals in December 2001). Although high CPUE values did occasionally occur, the data for each species were strongly skewed toward zero and very low CPUE values. The average percent of nonzero catches across all years analyzed was 28.1 % for delta smelt, 50.2 % for longfin smelt, 52.1 % for age-0 striped bass, and 47.1 % for threadfin shad (Fig. 2).

Sampling Covariates

Based on AIC statistics, the full zero-inflated negative binomial GLM (model M_4) received the most empirical support for each species (Table 1). For delta smelt, model M_5 received modest empirical support (ΔAIC=5.9), and for the other three species, no other parameterizations were comparatively supported. The superior performance of model M_4 suggested that all covariates were statistically important for each species and that CPUE and the probabilities of false zeros varied considerably by year, month, area within the delta, and across the domain of observed Secchi depths.

The model predicted yearly CPUE indices showed differing patterns for each species (Fig. 3). For delta smelt, higher predicted CPUE generally occurred in the early 1970s, 1980, and also for various years during the 1990s. The highest value occurred in 1991, and low CPUE was predicted for much of the 1980s and 2000s. Longfin smelt predicted CPUE was variable and high during the late 1960s, early 1970s, and for a few years during the early 1980s. Since 2000, predicted CPUE was consistently low with 2007 marking the lowest index value on record. Age-0 striped bass predicted CPUE consistently declined through time. The first year in the survey (1967) marked the highest age-0 striped bass predicted CPUE value on record while 2002 marked the lowest value. Threadfin shad predicted CPUE declined in the late 1960s, rebounded to higher but variable levels from the mid-1980s to early 2000s, and declined to the lowest value on record in 2012. Average species-specific CPUE across the time series was as follows: 1.24 fish/tow for delta smelt, 13.4 fish/tow for longfin smelt, 5.34 fish/tow for age-0 striped bass, and 22.9 fish/tow for threadfin shad. The precision of the estimated indices for all species was fairly low as bootstraped estimated

Table 1 Model selection statistics associated with the zero-inflated generalized linear models used to analyze catch-per-unit-effort data from the Fall Midwater Trawl survey for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad, 1967–2012. Covariate abbreviations: Y year, M month, A area, S Secchi depth; and nc indicates model failed to converge successfully. No sampling occurred in 1974, September 1976, December 1976, and 1979

Model	Count covariates	False zero covariates	No. par.	Delta smelt		Longfin smelt		Age-0 striped bass		Threadfin shad	
				AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
M_1	Y	Y	89	*nc*	*nc*	30,253.0	944.1	36,708.6	1299.4	24,364.7	1334.3
M_2	Y+M	Y+M	95	20,844.2	1348.6	29,751.4	442.5	36,630.4	1221.2	24,319.7	1289.4
M_3	Y+M+A	Y+M+A	103	19,872.9	377.3	29,602.4	293.6	36,038.7	629.5	23,336.2	305.8
M_4	Y+M+A+S	Y+M+A+S	105	19,495.6	0.0	29,308.9	0.0	35,409.2	0.0	23,030.3	0.0
M_5	Y+M+A+S	Y+M+A	104	19,501.5	5.9	29,323.0	14.1	35,423.5	14.3	23,246.9	216.7
M_6	Y+M+A+S	Y+M	100	19,795.0	299.4	29,356.0	47.1	35,537.2	128.0	*nc*	*nc*
M_7	Y+M+A+S	Y	97	19,801.9	306.3	29,690.6	381.7	*nc*	*nc*	23,332.8	302.3
M_8	Y+M+A	Y+M+A+S	104	19,635.3	139.7	29,497.7	188.8	35,677.2	268.0	23,045.0	14.6
M_9	Y+M	Y+M+A+S	100	19,795.2	299.6	29,588.6	279.7	35,988.1	578.9	23,956.3	926.0
M_{10}	Y	Y+M+A+S	97	19,834.8	339.2	29,601.4	292.5	36,137.9	728.7	23,993.2	962.8
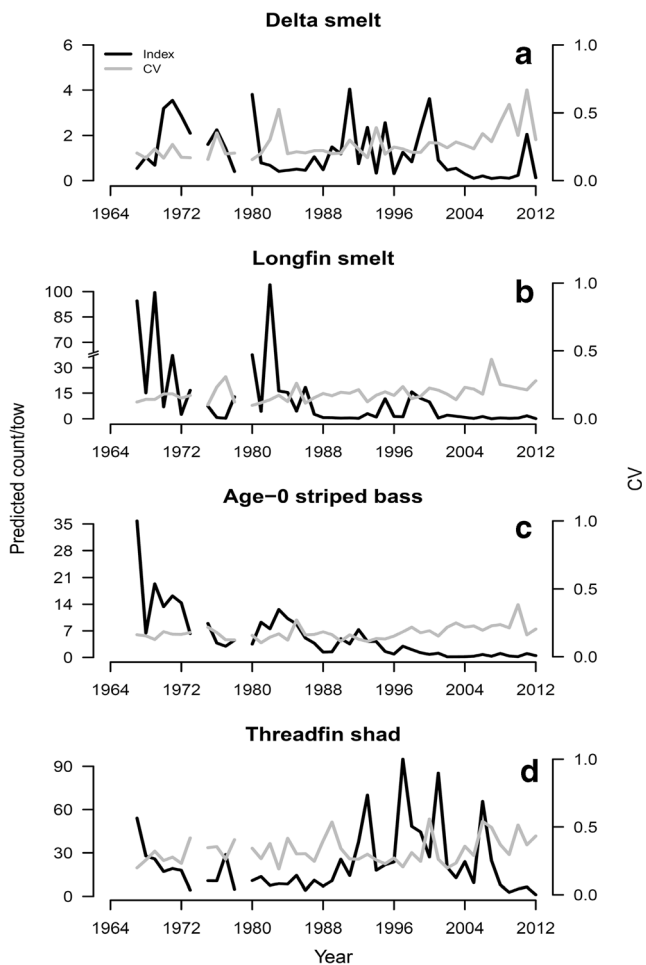
Fig. 3 Predicted yearly catch per unit effort (mean count per tow) and associated coefficients of variation (CV) based on zero-inflated generalized linear models applied to Fall Midwater Trawl survey data, 1967–2012, for **a** delta smelt, **b** longfin smelt, **c** age-0 striped bass, and **d** threadfin shad. No sampling occurred in 1974, September 1976, December 1976, and 1979. Note break in left *y*-axis for longfin smelt

yearly CVs predominately ranged between 0.15 and 0.45 with occasional values greater than 0.5.

Peak predicted monthly CPUE occurred in October for delta smelt, December for longfin smelt, September for age-0 striped bass, and November for threadfin shad (Fig. 4). Delta smelt predicted CPUE indices for November and December did not differ considerably from its peak month nor did the threadfin shad predicted December CPUE when compared to its peak. Spatially, highest predicted CPUE occurred in area 15 for delta smelt, area 12 for longfin smelt, area 15 for age-0 striped bass, and area 17 for threadfin shad. Age-0 striped bass predicted CPUE for areas 12 and 14 were comparably similar in magnitude to its peak.

The response in predicted CPUE across the range of observed standardized Secchi depths was strong and consistent across each species, as higher predicted CPUE values corresponded to low observed Secchi depths. This result emerged because the estimated Secchi depth coefficients associated with the count component of model M_4 were consistently negative across species. Related were the consistently positive estimated coefficients for the false zero model component of each species. Therefore, predicted CPUE declined with increased water clarity (higher Secchi depth) and the probabilities of false zeros increased with water clarity. In terms of actual water clarity conditions in the delta, the minimum observed Secchi depths for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad were 0, 0, 0, and 0.12 m, respectively, while the maximum were 2, 1.6, 2, and 2.09 m. Relative to the maximum predicted CPUE for each species, the observed Secchi depth at which estimated CPUE decreased by 25, 50, and 75 %, respectively, was approximately 0.07, 0.17, and 0.35 m for delta smelt, 0.10, 0.25, and 0.50 m for longfin smelt, 0.11, 0.23, and 0.53 m for age-0 striped bass, and 0.4,

Fig. 4 Predicted catch per unit effort (mean count per tow) by sampling month, area, and across the range of observed standardized Secchi depths, respectively, based on zero-inflated generalized linear models applied to Fall Midwater Trawl survey data, 1967–2012, for (**a–c**) delta smelt, (**d–f**) longfin smelt, (**g–i**) age-0 striped bass, and (**j–l**) threadfin shad. No sampling occurred in 1974, September 1976, December 1976, and 1979
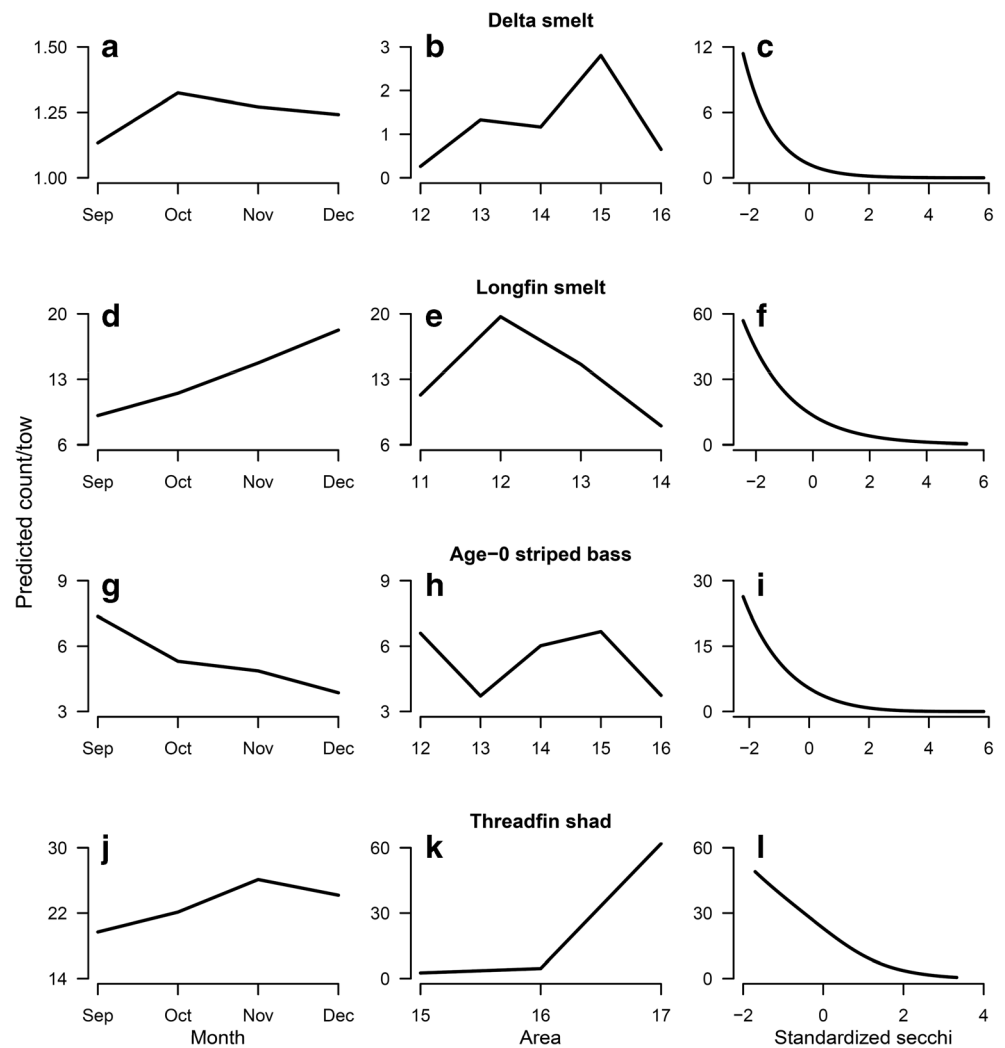

0.74, and 1.12 m for threadfin shad. Collectively, these results suggest that an increase from virtually no water clarity to roughly 0.5 to 1 m of water clarity corresponded to a 75 % or greater reduction in predicted CPUE for all species.

Annual Covariates

Predicted trends of the annualized biotic and abiotic variables showed differing patterns through time. Adult copepod density (calanoid, cyclopoid combined) has been variable but generally decreasing in the delta, with this trend being largely driven by taxa within the calanoid group (Fig. 5a–e). In contrast, the predicted trend in cyclopoid copepod density has been increasing since the mid-1990s; however, the comparably low density of cyclopoid copepods marginalized the impact of this group on the combined copepod trend. Estimated mysid density has been fairly stable since 1990 but much reduced from peak and moderate levels in the mid-1980s and late 1970s, respectively. The predicted trend of chl-a was relatively high and variable in the early part of the time

series but considerably lower and more stable since 1987, which is when the lower trophic level food web of the delta changed in response to impacts by the introduced clam *Cobubula amurensis* (Kimmerer 2002).

Trends in predicted mean summer and winter water temperatures were generally stable over time, with estimated mean winter temperatures being slightly more variable than mean summer temperatures (Fig. 5f–j). Predicted trends of TSS, VSS, and turbidity in the delta were similar in that they showed considerable declines since the mid-1970s. Patterns in the various water flow variables showed distinct periods of "wet" and "dry" delta hydrology over time. Peak flow events occurred in 1983, the mid-1990s, and more recently in 2006, while low flows were observed in mid-1970s, early 1990s and late 2000s (Fig. 6). As expected, comparisons of type-specific (historical, unimpaired) patterns of inflows and outflows were generally the same qualitatively, with the latter simply reflecting reductions in water volume due to utilization. For the historical inflows and outflows, the two chosen averaging periods yielded virtually the same yearly volumes; however,
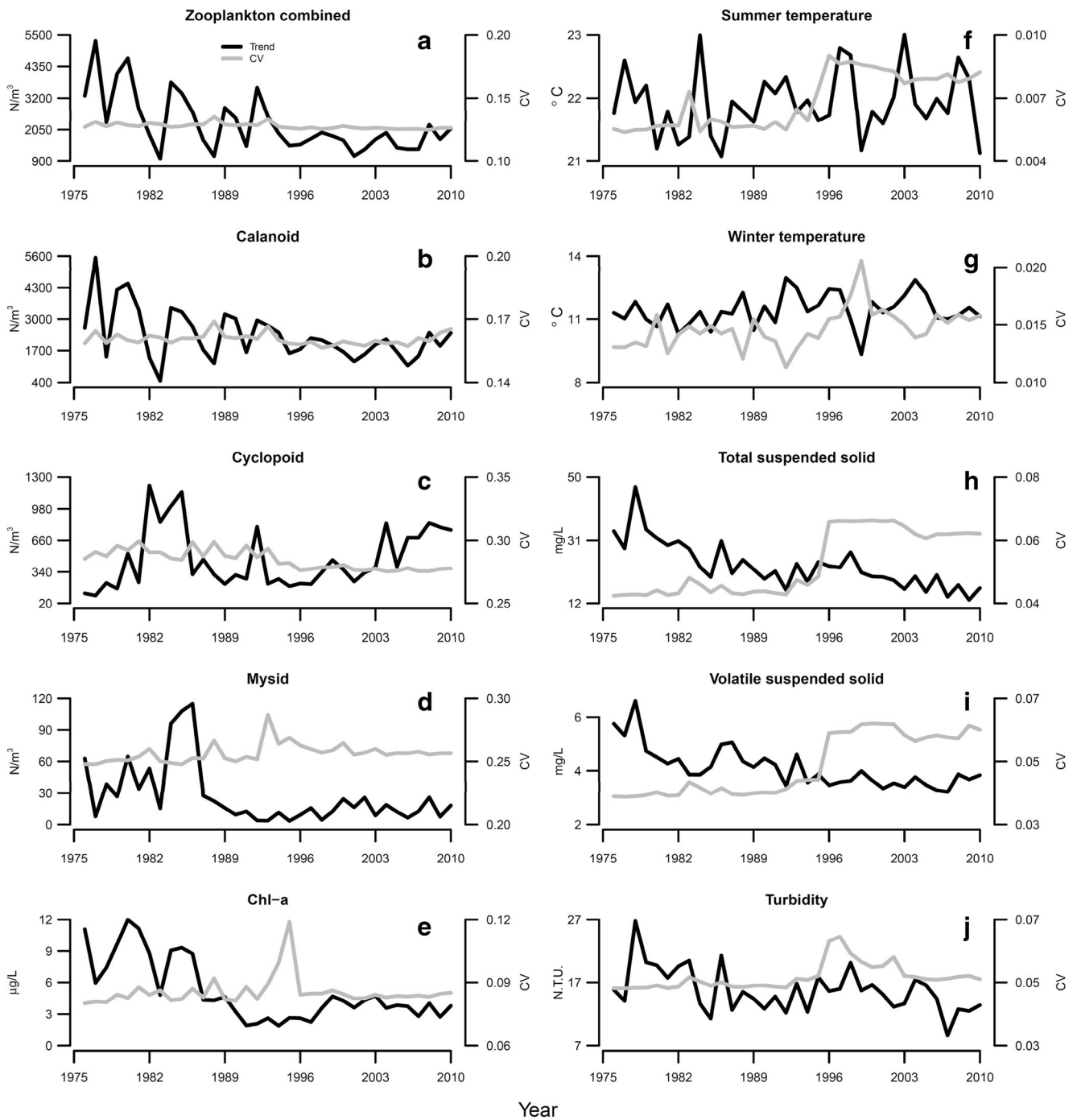
Fig. 5 Annualized mean trends and associated coefficients of variation (CV) based on various linear and generalized linear models fitted to zooplankton and discrete water quality data, 1976–2010, for **a** zooplankton combined (adult calanoid copepod and adult cyclopoid), **b** adult calanoid, **c** adult cyclopoid, **d** mysid, **e** chl-*a*, **f** summer water temperature (Jul–Sep), **g** winter water temperature (Jan–Mar), **h** total suspended solid, **i** volatile suspended solid, and **j** turbidity

there were notable differences in yearly volumes of unimpaired inflow and outflow depending on the monthly averaging period. The precision of all estimated biotic and abiotic covariates was very good as evidenced by consistently low CVs.

Based on AIC statistics, the annualized variable TSS received the most empirical support for all species (Table 2).

Comparatively, there was no empirical support for any other annualized prey, water quality, or flow covariates. Predicted CPUE and probabilities of false zeros across the range of TSS were similar for three of the four species, with the exception being the predicted CPUE for threadfin shad (Fig. 7). Over the range of TSS, predicted delta smelt, longfin smelt, and age-0 striped bass CPUE increased, while the CPUE trend for

Fig. 6 Annualized trends in flow averaged monthly from January–June and March–May for **a** historical inflow, **b** historical outflow, **c** unimpaired inflow, and **d** unimpaired outflow. Flow variables lagged by 1-year are not shown
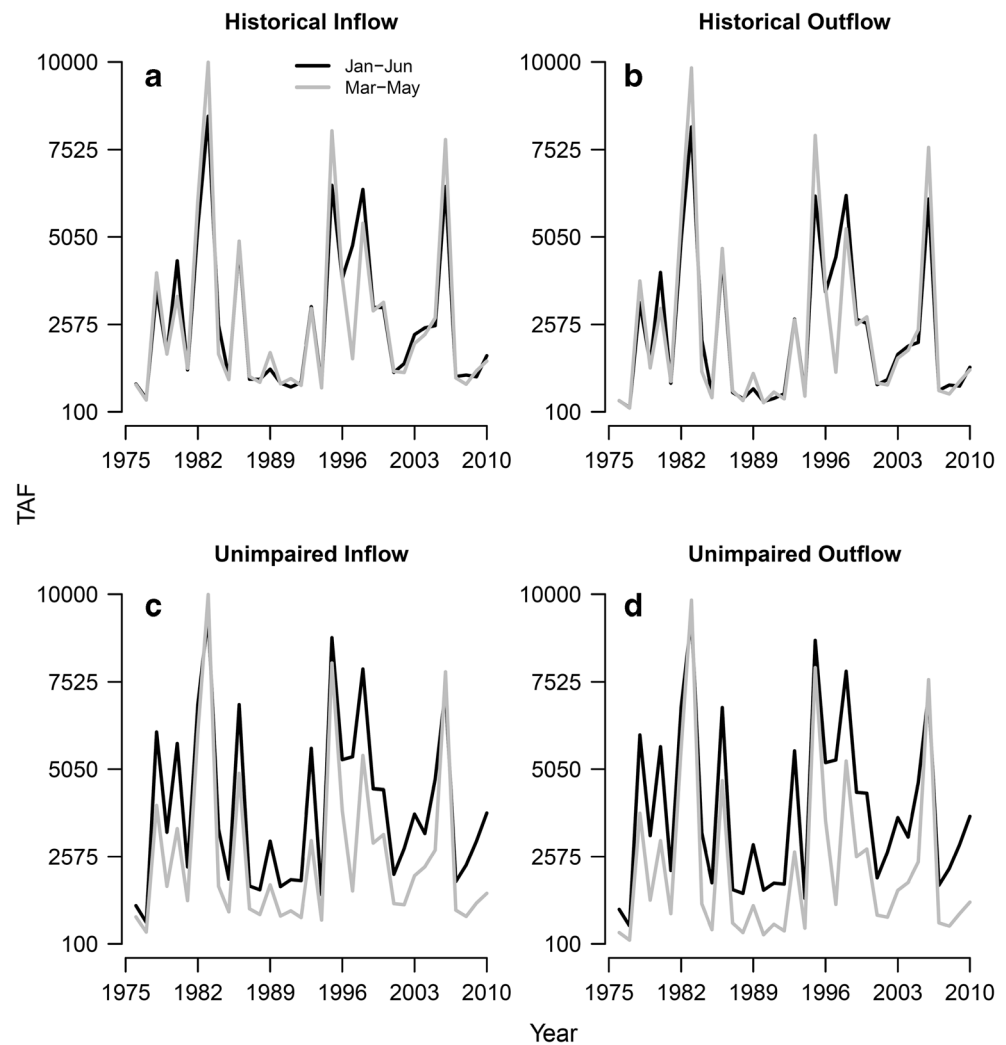
threadfin shad showed an inverse relationship. For all species, the predicted trends in probabilities of false zeros were fairly pronounced and decreasing with TSS. In terms of precision, the bootstrapped prediction intervals for both model components were generally narrow for all species.

Discussion

Sampling Covariates

Use of statistical models to quantify the importance of spatio-temporal and environmental covariates on survey CPUE can aid in understanding the dynamics of fish populations. For all species, the covariates year, month, region, and Secchi depth were important in explaining patterns in the observed CPUE data, particularly the zeros. However, relability of the results presented herein directly depends on satisfying the underlying modeling assumptions. For each species, plots of residuals for the count and false zero model components across the

observed domains of the covariates showed no distinct patterns, and overdispersion was adequately handled by the zero-inflated model structure. Therefore, from a model diagnostics perspective, the means of the negative binomial and binomial distributions appear to be well estimated. In terms of precision, bootstrapped CVs of the predicted yearly CPUEs were fairly low for all species and likely due to the relatively high sampling intensity of the FMWT survey and the high proportion of consistently low observed CPUE values. However, the CV estimates do depend on the assumption that gear catchability (defined as q in the equation $CPUE_y = qN_y$) has remained constant over time and space, so it is possible that they are optimistic. Since the inception of the FMWT survey, the number of monthly sampling locations has grown considerably (~25 %), yet accompanying studies of potential gains/losses in bias and precision of predicted CPUE are absent from the literature. In general, model-based approaches can be useful in the design of fishery-independent surveys (Peel et al. 2013), and the methods in this study could support optimization studies to evaluate design elements, appropriate

Table 2 Model selection statistics associated with the zero-inflated generalized linear models used to evaluate the biotic and abiotic annualized covariates for delta smelt, longfin smelt, age-0 striped bass, and threadfin shad, 1976–2010

Model	Annual covariate	Delta smelt		Longfin smelt		Age-0 striped bass		Threadfin shad	
		AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
A_1	Adult calanoid copepods	15,122.3	304.1	24,968.2	1642.2	27,545.5	691.4	19,325.6	263.8
A_2	Adult cyclopoid copepods	15,080.4	262.2	24,419.8	1093.8	27,420.7	566.6	19,247.5	185.7
A_3	Adult calanoid, adult cyclopoid combined	15,105.3	287.1	24,896.4	1570.3	27,433.2	579.1	19,310.9	249.1
A_4	Mysids	15,164.8	346.6	24,145.5	819.4	27,125.5	271.4	19,322.2	260.4
A_5	Chl-a	15,070.8	252.5	23,758.9	432.9	26,932.9	78.7	19,326.7	264.9
A_6	Summer temperature	15,113.2	295.0	24,633.0	1306.9	27,536.3	682.2	19,311.5	249.7
A_7	Winter temperature	15,095.2	277.0	24,282.6	956.5	27,472.6	618.5	19,325.3	263.5
A_8	Total suspended solids	14,818.2	0.0	23,326.1	0.0	26,854.1	0.0	19,061.8	0.0
A_9	Volatile suspended solids	15,074.5	256.3	24,612.9	1286.8	27,106.2	252.1	19,213.2	151.3
A_{10}	Turbidity	14,853.1	34.8	23,449.7	123.6	27,493.2	639.0	19,196.7	134.9
A_{11}	Historical outflow Jan–Jun	14,974.3	156.0	23,509.0	183.0	27,390.9	536.8	19,288.4	226.6
A_{12}	Historical outflow Mar–May	15,067.4	249.1	23,766.1	440.0	27,396.4	542.3	19,318.2	256.4
A_{13}	Historical outflow Jan–Jun, 1-year lag	15,164.2	346.0	24,872.2	1546.1	27,521.8	667.7	19,316.3	254.5
A_{14}	Historical outflow Mar–May, 1-year lag	15,158.5	340.3	24,925.1	1599.0	27,536.0	681.8	19,330.4	268.6
A_{15}	Historical inflow Jan–Jun	14,975.6	157.3	23,497.8	171.8	27,394.6	540.5	19,290.8	229.0
A_{16}	Historical inflow Mar–May	15,065.6	247.4	23,707.9	381.9	27,387.8	533.6	19,317.2	255.3
A_{17}	Historical inflow Jan–Jun, 1-year lag	15,162.8	344.6	24,879.9	1553.8	27,524.4	670.2	19,315.9	254.1
A_{18}	Historical inflow Mar–May, 1-year lag	15,158.4	340.1	24,929.6	1603.5	27,531.7	677.6	19,329.0	267.2
A_{19}	Unimpaired outflow Jan–Jun	14,989.8	171.6	23,615.2	289.1	27,436.2	582.1	19,315.2	253.3
A_{20}	Unimpaired outflow Mar–May	15,025.4	207.2	23,968.6	642.5	27,451.5	597.4	19,331.6	269.8
A_{21}	Unimpaired outflow Jan–Jun, 1-year lag	15,167.2	349.0	24,899.4	1573.3	27,549.8	695.7	19,317.4	255.5
A_{22}	Unimpaired outflow Mar–May, 1-year lag	15,152.6	334.4	24,944.6	1618.5	27,557.8	703.7	19,329.1	267.3
A_{23}	Unimpaired inflow Jan–Jun	14,989.9	171.7	23,613.4	287.3	27,436.7	582.6	19,315.4	253.5
A_{24}	Unimpaired inflow Mar–May	15,025.5	207.2	23,969.1	643.0	27,452.3	598.1	19,331.6	269.8
A_{25}	Unimpaired inflow Jan–Jun, 1-year lag	15,167.1	348.9	24,899.4	1573.3	27,550.0	695.9	19,317.4	255.6
A_{26}	Unimpaired inflow Mar–May, 1-year lag	15,152.7	334.5	24,944.3	1618.2	27,558.3	704.2	19,329.0	267.2

sample sizes, and allocation of resources for future FMWT surveys. The estimated monthly, regional, and Secchi depth effects generated relatively unique predicted CPUE patterns for each species, which can, in turn, be used as important foundational information for future hypothesis-driven field studies and mechanistic modeling activities.

The annual frequency of zero CPUE observations over the course of the entire FMWT survey was appreciably high for all species (Fig. 2). As a means of coarsely evaluating the temporal pattern of zero inflation in the FMWT data, model M_4 and its nonzero-inflated counterpart (intercept only parameterization for the false zero component) were sequentially fitted to subsets of the FMWT data set truncated by decade for each species. That is, the two models were applied to only 1960s data, then to 1960s–1970s data, then to 1960s–1980s data, and so on through the full time series. With the exception of the 1960s data for longfin smelt, AIC statistics strongly supported the zero-inflated parameterization for all species and time periods. Therefore, it appears that the FMWT survey

data have almost always contained more zero CPUE observations than would otherwise be expected given a negative binomial count process, which raises the question, why?

Failing to successfully encounter target populations can arise because they are rare, samples are taken in suboptimal habitats (true zeros), or because samples are taken in optimal habitats but reduced survey catchability across time, space, and/or ecosystem conditions prevent successful collections (false zeros). For delta smelt, rarity may be a plausible explanation, especially given that the highest predicted yearly CPUE was only 4.04 fish per tow and the 45-year average was just 1.24 fish per tow. However, species rarity does not seem likely for the other three fishes given that predicted yearly longfin smelt CPUE values early in the time series were very high (>70 fish per tow), estimated adult striped bass abundance exceeded 1 million fish in the early 1970s (Stevens et al. 1985) thus requiring considerable age-0 production, and threadfin shad have been viewed as highly abundant since appearing in the delta (Feyrer et al. 2009).
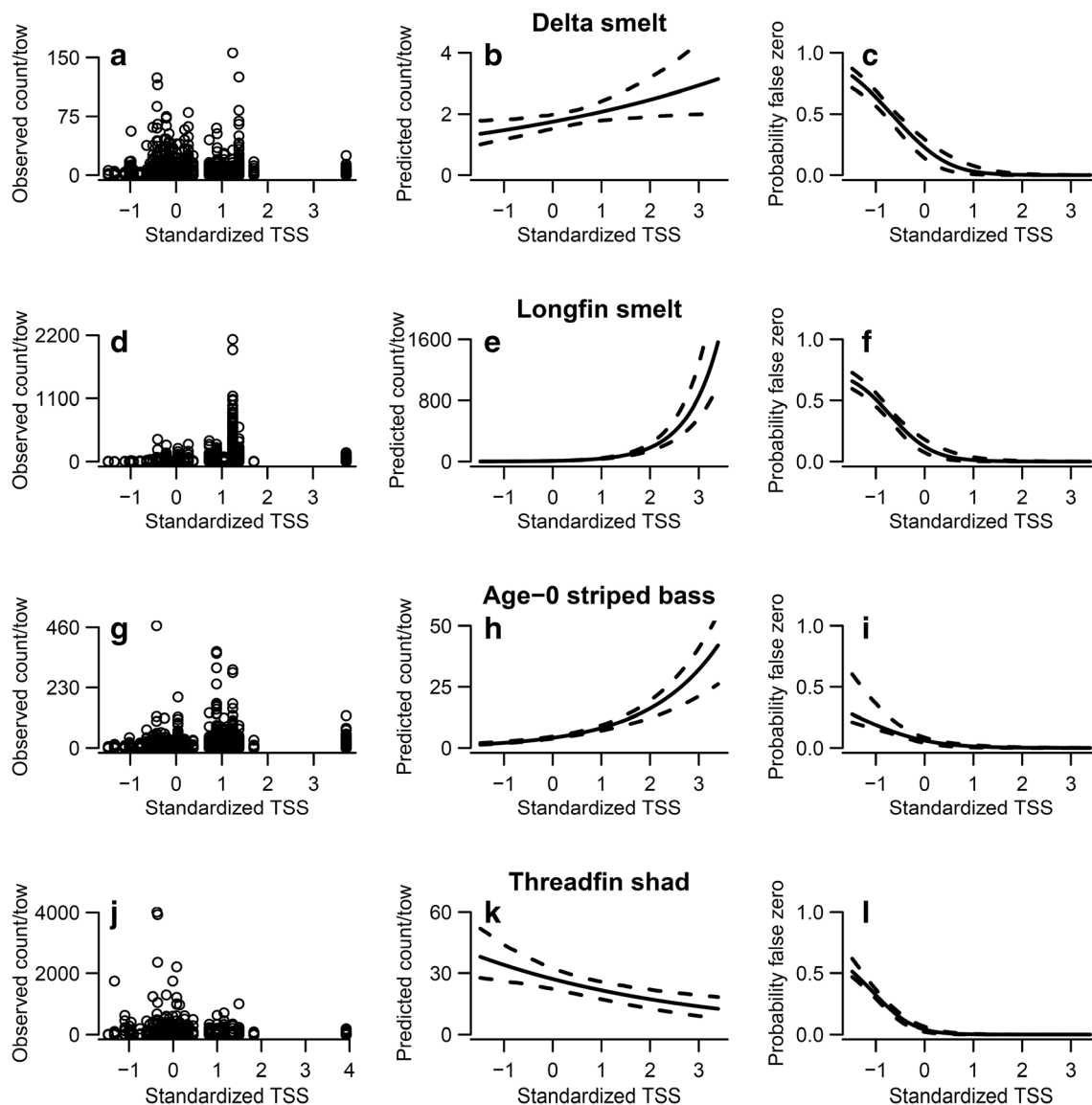
Fig. 7 Observed catch per unit effort (CPUE, mean count per tow, *left panels*), predicted CPUE (*middle panels*), and predicted probabilities of false zeros (*right panels*) with 95 % prediction intervals across observed standardized TSS for (**a–c**) delta smelt, (**d–f**) longfin smelt, (**g–i**) age-0 striped bass, and (**j–l**) threadfin shad

The FMWT survey does follow a fixed station sampling design, which raises the possibility that samples are consistently taken at locations that do not support high localized fish abundance. Additionally, if habitat utilization of fishes in the delta has systematically changed over time in response to morphological alterations of the estuary and/or sustained regimes of ecosystem conditions, differences in CPUE and distribution become confounded. The relatively high spatiotemporal sampling intensity of the FMWT survey may somewhat mitigate these concerns, but the four focal species are schooling pelagic fishes, and thus, variable distributions through time and space should be expected.

The consistency of the model prediction to Secchi depth for all species warrants deeper consideration, especially in the

context of false zeros. Feyrer et al. (2007) analyzed raw FMWT survey data to evaluate fish occurrences (presence/absence of delta smelt, age-0 striped bass, and threadfin shad) in relation to various environmental variables and documented an inverse response with Secchi depth. Feyrer et al. (2011) updated that analysis and extended it to derive habitat index values for delta smelt (but see comments provided Manly et al. (2015)). The results of this study generalize the importance of Secchi depth to include CPUE. Feyrer et al. (2007) noted that higher presence/absence of delta smelt at lower Secchi depths could be due to required turbidity for feeding and/or turbidity mediated top-down predation impacts. A third potential explanation is that catchability of the FMWT survey sampling gear changes with Secchi depth. In general, Secchi depth is a coarse measurement of water clarity, and it is not possible to

distinguish among constituent groups causing low measurements. If those constituent groups are largely organic material, then a positive fish CPUE response to food availability is possible. Conversely, if those constituent groups are not largely organic, then higher CPUE at lower Secchi depths could be due to compromised foraging impacts of visually oriented piscivores such as larger striped bass (Horodysky et al. 2010). However, all of the fishes in this study are pelagic, planktivorous feeders, and thus, it is reasonable to assume that vision plays a central role in their sensory ecology. Animals could be more effective at gear avoidance under higher Secchi depths than at lower Secchi depths simply because of a larger field of visibility for gear detection.

Although experimentally testing the variable catchability hypothesis is challenging, flume trials to assess gear behavior under various hydrographic conditions, video equipment attached to sampling gear, and coordinated field studies using multiple survey gears designed to quantify relative catchabilities could be informative. Additional modeling efforts may also assist in identifying and quantifying covariate effects on relative catchability. In terms of the bottom-up hypothesis, characterization of water column constituents synoptic with fish stomach content analysis could assist in understanding trophic interactions and prey selectivity, which could aid in determining if the inverse relationship of CPUE and Secchi depth is a response to food availability. Regarding top-down impacts, results of striped bass and other fish predator diet composition studies in the delta have shown very little consumption of delta smelt and longfin smelt, and modest consumption of age-0 striped bass and threadfin shad (Nobriga and Feyrer 2007; Nobriga and Feyrer 2008). However, these studies were temporally abbreviated, and each acknowledged potential biases due to spatial limitation of predator stomach collections. Therefore, systematic temporal and spatial diet composition studies of piscivorous fishes could be helpful in more fully understanding predation impacts of larger fishes.

Annual Covariates

The annualized covariates considered were chosen in an effort to evaluate the effects of hypothesized covariates on fish CPUE that were potentially operating at an annual timescale. The choice to focus on the annual timescale was motivated from the notion that yearly environmental conditions have the potential to impact early life history and thus new year class formation. However, the analytical approach taken here to evaluate annual covariates can be used for variables aggregated across other potentially meaningful scales. For example, biotic or abiotic variables summarized monthly or seasonally could be used to more directly explore drivers of within-year CPUE patterns, and variables could be aggregated spatially to

investigated rivers of fish distribution within the delta. Studies of this type represent fruitful areas of future research.

The strong empirical evidence supporting TSS as the best annualized covariate for all species is consistent with the importance of Secchi depth documented in the analysis of sampling covariates. Trends in the model predicted CPUEs and probabilities of false zeros across TSS were analogous to those associated with Secchi depth, with the exception of predicted threadfin shad CPUE which showed a modest decline with TSS. Inspection of the raw threadfin shad CPUE data in relation to TSS showed relatively high frequencies of both zero (>50 % of the tows analyzed) and large CPUE values (>100 fish per tow, 3.9 % of the tows analyzed) at low TSS values when compared to high TSS values. The collective presence of these relatively infrequent large observed CPUEs and numerous observed zero CPUE values likely created the declining predicted CPUE and probability of false zero relationships with TSS (Fig. 7k). The results for the other three species strongly confirm the effect that more turbid water yields higher predicted CPUE and demonstrates that it is also detectable at an annual timescale. As a stand-alone result, the concept that water clarity mediates CPUE keeps the bottom-up, top-down, and variable gear catchability hypotheses in play; however, the strong support for the annualized TSS covariate combined with the lack of empirical support for any of the annualized prey covariates and the aforementioned relative absence of the focal fish species in predator diets may favor the variable catchability hypothesis.

Much of the contemporary understanding regarding covariate effects on fish CPUE in the delta has revolved around flow, particularly outflow and the location of X_2. In this study, X_2 was not considered largely because it is highly variable, often moving significant distances within a single tidal cycle (pers. com., W. Bourez, MBK Engineers, Sacramento, CA) and because it is a proxy covariate directly influenced by flow. Thus, inclusion of the various flow covariates constitutes a more direct evaluation of delta hydrology. CPUE indices of pelagic fishes in the delta have been showed to be positively related to delta outflow (Kimmerer 2002; Sommer et al. 2007), but it is important to note that higher flow regimes lead to higher TSS concentrations. For the data in this study, the historical outflow January–June and March–May time series are each positively correlated with TSS and signficant at the $\alpha = 0.07$ level (Pearson's product moment correlations, $\rho_{JJ} = 0.32$ [$p = 0.058$], $\rho_{MM} = 0.31$ [$p = 0.067$]). Therefore, higher delta outflow leads to poorer water clarity, which, in turn, could increase survey gear catchability and lead to higher estimated yearly CPUE indices.

If the annualized covariates analysis is restricted to only include the flow covariates, the results indicated that historical outflow averaged January–June received the most support for delta smelt and threadfin shad, and historical inflow averaged January–June and averaged March–May were best supported

for longfin smelt and age-0 striped bass, respectively (Table 2). However, there was competing empirical support for historical inflow averaged January–June for delta smelt (ΔAIC=1.3) and for historical outflow averaged January–June (ΔAIC=3.1) for age-0 striped bass. Collectively, these results fail to confirm the effect of a single dominant flow covariate on fish CPUE in the delta, which is arguably not surprising since the underlying dynamics of the focal fish species are likely shaped by intersections of a complex suite of biological, ecological, and environmental processes.

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