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RESEARCH

An Evaluation of Three Fish Surveys in the San Francisco Estuary, California, 1995–2015

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ABSTRACT

Resource managers rely on long-term monitoring surveys conducted in the San Francisco Estuary to evaluate the status and trends of resident fish populations in this important region. These surveys are potentially confounded because of the incomplete detection of individuals and species, the magnitude of which is often related to the same factors that affect fish populations. We used multistate occupancy estimators to evaluate the distribution, abundance, and detection probability of four fish species collected during 1995–2015 with three long-term surveys. Detection probabilities varied positively with fish abundance and negatively with Secchi depth. Detection varied among species and was greatest for the 20-mm Survey and least for the midwater trawl used for the midwater trawl used in the San Francisco Bay Study. Incomplete detection resulted in underestimates of occupancy and abundance across species and surveys and were greatest for the Bay Study. However, trends in occupancy and abundance of the study period appeared to be unbiased. Fish occupancy and abundance were generally related to salinity or specific conductance, day-of-the year, and water temperature, but the nature of the relations varied among surveys and species. There also was strong spatial and temporal dependence in species-specific occupancy and abundance that changed through time and were unrelated to the covariates considered. Our results suggest that managers consider incorporating methods for estimating detection and adjusting data to ensure data quality. Additionally, the strong spatio-temporal patterns in the monitoring data suggest that existing protocols may need to be modified to ensure that data and inferences reflect system-wide changes rather than changes at a specific set of non-randomly selected locations.

KEY WORDS

Incomplete capture, multistate occupancy, systematic bias, trends, Delta Smelt, Longfin Smelt, Striped Bass, Sacramento Splittail

INTRODUCTION

Changes to habitats, water quality, and hydrologic regimes that are associated with anthropogenic development and climate change have been identified as some of the foremost threats to fishes and other aquatic biota in estuarine ecosystems. Natural resource managers can be effective at mitigating or minimizing such threats to fishes only if they are informed as to the current status and recent trends in fish populations as well as the nature and extent of potential detrimental impacts (e.g., climate change). The ability to determine the population status and trends and the effectiveness of fish conservation strategies depends upon the quality of the fish monitoring data (Peterson and Rabeni 1995). Sampling bias and variance are the primary factors that influence the quality of these data and hence, the ability of managers to make informed decisions.

When sampling fish populations, individuals and species within a sample unit are generally not all captured or detected (Peterson and Paukert 2009). The ability to capture fishes is reportedly related to factors such as sampling method; fish size, morphology and behavior; and the physical and chemical characteristics of sample units. Failure to account for incomplete capture introduces a systematic error or negative bias into the data. As noted by Hurlbert (1984), systematic error can significantly affect the validity of inferences from experiments or observational studies. While many fishery biologists acknowledge the presence of sampling bias and its potential to substantially affect point estimates of population abundance, it is often believed that biased data are still useful for examining "trends" in the resource. Despite this paradigm, rigorous evaluations of population abundance indices uncorrected for incomplete detection indicate that analyses of time trends can be biased (Thompson 2002). Indeed, systematic bias related to fish capture is particularly problematic when the factors affecting fish capture are the same factors affecting fish population processes or are factors that change systematically in space and time (Peterson and Paukert 2009). For example, Thurow et al. (2006) found that the ability to detect salmonids during snorkel surveys depended on turbidity and water temperature, two factors that co-vary with discharge. They further showed that trends in annual discharge across the Intermountain West potentially induced a systematic bias in salmonid snorkel survey data. Thus, reliance on biased estimates of fish population size to infer population status and trends, and to parameterize models of fish population response to management actions or environmental variation could lead to poor resource management decisions and the development of ineffectual policies and regulations for conserving aquatic species.

Studies performed in the San Francisco Estuary give typical examples of the potential influence that data quality can have on perceived changes to fish communities. Fish population monitoring has been conducted throughout the estuary since the late 1950s using a variety of active sampling gear. These surveys were originally developed to assess the status and trends in economically and recreationally important species, such as juvenile salmon and Striped Bass *Morone saxatilis*. However, evaluations of trends in population indices calculated using these data suggest strong decreases in abundance of target and non-target species over time, particularly pelagic fishes that include the federally listed Delta Smelt *Hypomesus transpacificus* and Longfin Smelt *Spirinchus thaleichthys* and Striped Bass (Sommer et al. 2007; Cloern and Jassby 2012). These reported declines have been attributed to widespread changes in the estuary during the monitoring period, including: changes in water quality (Thompson et al. 2000); invasion by exotic species (Kimmerer and Orsi 1996); habitat alteration (Baxter et al. 2010); and changes associated with human water use and diversion (Kimmerer 2008; Sommer et al. 2011). The indices of abundance used by these studies are not adjusted to account for incomplete capture and are likely negatively biased to some extent. It remains to been seen if these sample biases are also related to changes in the estuary such that inferences about trends in population dynamics are confounded by trends in capture probability. For example, systematic trends in water clarity (Barnard et al. 2013) and temperature (Jassby 2008) have been observed in the estuary and both factors have also been shown to affect the ability of researchers to capture fishes (Bayley and Peterson 2001; Peterson et al. 2004; Price and Peterson 2010). Similarly, changes in gear and sampling procedures that presumably resulted from personnel rotation and equipment upgrade/

repair across the decades-long monitoring also can impose a systematic bias in the data (Peterson and Paukert 2009). Thus, there remains a need to evaluate the potential biases in existing monitoring protocols and sample designs used in the estuary and if necessary, develop alternative approaches and estimators.

An evaluation of potential sample biases requires an unbiased estimate of the known number of fish within a sample unit. Previous evaluations have used three basic approaches to obtain these estimates: (1) by introducing a known number of fish into a sample unit; (2) by collecting fish within a site, marking, and returning them; and (3) using an unbiased population estimator (Peterson and Paukert 2009). Of these, the last approach is the most feasible for evaluating the reliability of the population status and trends information derived from long-term estuary studies. A variety of estimators are available for estimating the abundance, distribution, and capture (or detection) probability of unmarked fishes, but these estimators require the collection of replicate samples from study sites that are assumed to contain closed populations (i.e., no births, deaths, emigration, and immigration). Of the 16 surveys currently conducted in the estuary, only three– the 20 mm Survey, San Francisco Bay Study (Bay Study), and Summer Townet Survey—consistently collect multiple samples (tows) during each survey. All three of these studies have been conducted for more than two decades. Despite the significant expenditure of time and resources to collect these data, there has been no comprehensive evaluation of the efficiency or effectiveness of long-term monitoring protocols for assessing the abundance and distribution of fishes of concern (see however Mahardja et al. 2017). Therefore, our objectives were threefold: (1) evaluate the efficiency of the sampling methods used and identify factors that affect fish capture, (2) estimate the historical distribution and abundance of fishes, and (3) evaluate potential systematic biases in historic estimates of abundance and distribution and identify the likely sources of the biases.

MATERIALS AND METHODS

Study Area

The San Francisco Estuary is the largest estuary on the Pacific Coast and supports more than 500 fish, wildlife and plant species, including several threatened and endangered species. The eastern end of the estuary historically consisted of extensive marsh-wetland complexes at the confluence of the Sacramento and San Joaquin rivers, but was converted to agricultural land uses beginning in the mid-19th century. During this time, levees were constructed along stream channels and islands to help protect water exports from saltwater intrusion (Galloway et al. 1999). Water from the Sacramento–San Joaquin Delta flows westerly through San Pablo Bay and San Francisco Bay into the Pacific Ocean (Figure 1). There are additional freshwater inputs to the estuary from several tributaries including the Petaluma, Napa, and Guadalupe rivers.

Data

Since 1995, the 20-mm Survey has been conducted from early spring (March and April) to mid-summer (July and August). The objective of the survey is to evaluate the distribution and abundance of Delta Smelt and their prey and assist in the estimation of fish losses because of entrainment at of the State Water Project and the Central Valley Project. Samples are collected every other week resulting in typically 8–10 surveys at each station per year. Up to 55 stations per year have been sampled, but only 41 stations, referred to as index stations, have been consistently sampled since 1995 and were the only 20-mm Survey stations included in our analysis. Larval and juvenile fish are sampled using a 5.5 m long conical plankton net with 1.59 mm mesh, and 1.51 m^2 mouth opening (Honey et al. 2004). A flow meter is mounted in the mouth of the net to estimate the volume of water sampled. Each station is sampled using three consecutive 10-min stepped oblique tows. The contents of each tow are transferred to a sample jar and brought to a laboratory for fish identification and quantification.

The Summer Townet Survey began in 1959 with the objective of indexing the relative abundance of Striped Bass, but has since been used to evaluate

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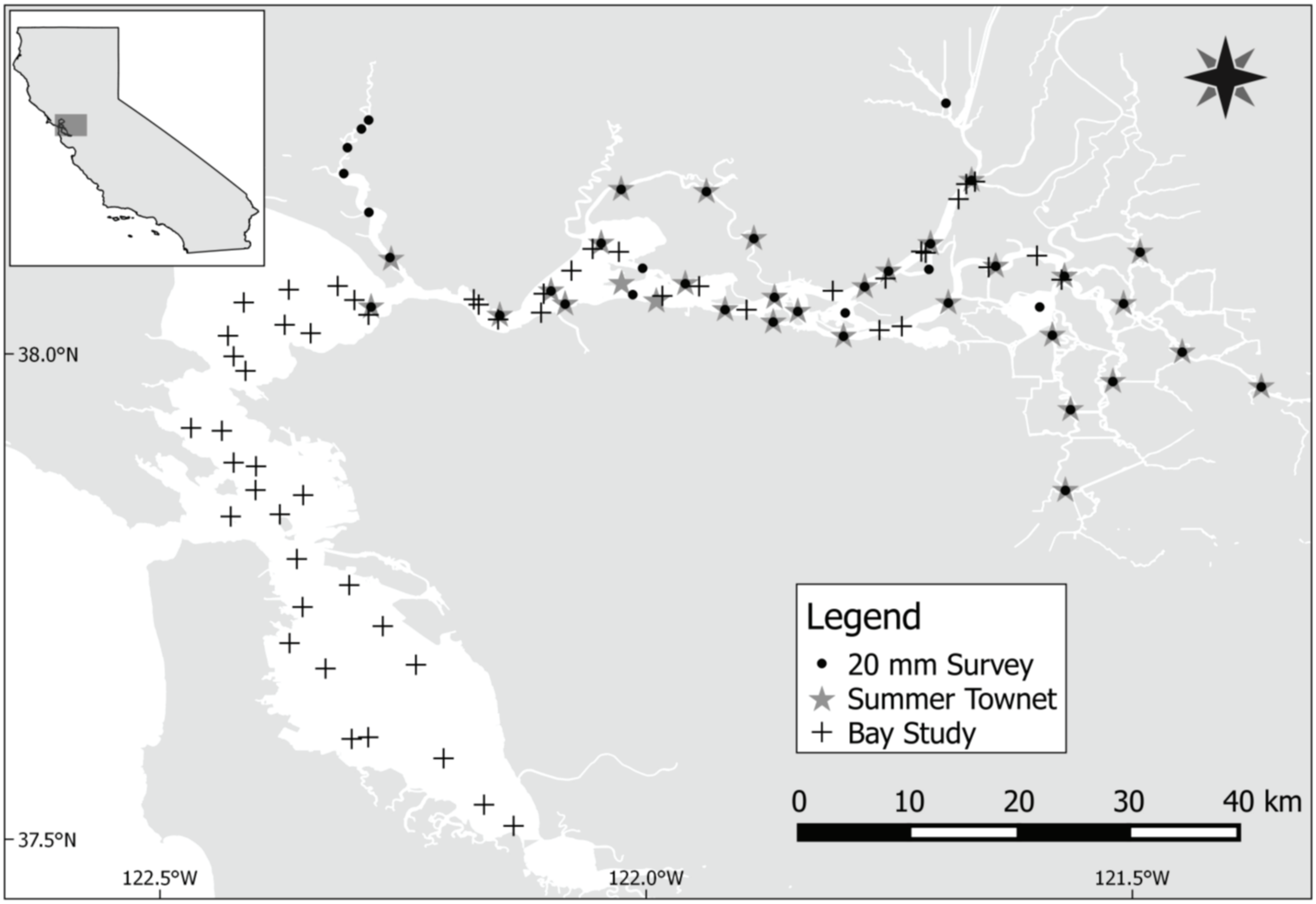

Figure 1 Map of the San Francisco Estuary and the long-term study sites used in the analysis of fish abundance, distribution, and detection

status and trends in Delta Smelt. Before 2003, 2–5 surveys were conducted at 32 stations annually from approximately June to August. The number of surveys was standardized to 6 per year in 2003. An additional 8 stations were added in 2011, resulting in 40 stations (Figure 1) that were included in our analysis. Fishes were sampled during the Summer Townet Survey using a "D" frame with a 1.49 m^2 opening that consisted of an outside 12.7 mm mesh section approximately 15 m long and a woven nylon fyke inside of the netting (Honey et al. 2004). The volume of each tow from 1970–2002 was calculated based on mouth area, net speed, and distance towed. Beginning in 2003, a flow meter, mounted at the mouth of the net, was used to estimate the volume sampled. A minimum of two oblique tows are made against the current, if present, with an additional third tow if fish are detected in at least one of the first two tows at each station.

The Bay Study began in 1980. The purpose of the study was to evaluate the effects of freshwater outflow on fish and invertebrates in the estuary. Surveys are generally conducted monthly throughout the year at (currently) 52 stations (Figure 1) and employ two different gears, a midwater trawl and otter trawl. The midwater trawl is intended to primarily sample pelagic fishes, while the otter trawl is primarily intended to sample demersal fishes, shrimp, and crabs. The midwater trawl consists of a 3.7 m^2 mouth with 20.5 cm mesh that gradually reduces to 1.3 cm mesh codend (Armor and Herrgesell 1985). It is towed obliquely with the current for approximately 12 min. The volume of the water filtered is calculated using the mouth area and distance towed relative to the current as measured by a flow meter that is suspended off the side of the boat. The otter trawl consists of a 4.9 m head rope with 2.5 m mesh body and 1.3 cm mesh codend (Armor and Herrgesell 1985). The otter trawl is towed after sampling with the midwater trawl. It is towed on the bottom and against the current for approximately 5 min. The distance towed with the otter trawl was estimated with Loran C or GPS.

In conjunction with sampling, crews took several physiochemical measurements, in addition to tow distance, duration, volume of water sampled, and time of sampling. Many of the same measurements were consistently collected across all surveys. Specific conductivity (μs cm^{-1}) and water temperature (°C) within 0.3 m of the surface and within 0.3 m of the bottom were made with calibrated meters. The top and bottom values also were averaged. Secchi depth (cm) and bottom depth (m) also were measured and recorded. Tides were recorded as: high (slack), ebb, low (slack), and flood and wave conditions as: calm, waves with no whitecaps, and waves with whitecaps. Salinity (ppt) was consistently collected at the surface and bottom for the Bay Study only and surface turbidity (NTU) for Summer Townet Survey only. These data were compiled to evaluate the effect of habitat and water quality characteristics on fish distribution and abundance. We also calculated the position of the X2 isohaline using the methods in Hutton et al. (2015). For each survey, we calculated the amount of time (h) after sunrise that a sample (tow) was collected using the sunrise times at Rio Vista CA (NOAA 2016). Finally, we calculated the order in which samples were collected each day to allow an evaluation of changes in gear effectiveness through time during each sample day.

One of our objectives was to evaluate potential biases in fish abundance and distribution trends across methods. Therefore, we analyzed survey data collected over two decades, 1995–2015, because these are the earliest dates when data were available for all three surveys. We also restricted our analyses to four fish taxa that are of considerable interest in the estuary: Delta Smelt, Longfin Smelt, Striped Bass, and Sacramento Splittail (*Pogonichthys macrolepidotus*). These species exhibit life histories and behaviors that may affect their vulnerability to the sampling gears. Delta Smelt is a resident estuarine species that is believed to be pelagic, using primarily open water habitats (Sommer et al. 2007) and are likely vulnerable to trawls towed through the water column. Longfin Smelt are also believe to be pelagic (Sommer et al. 2007), but they have greater saltwater tolerance than Delta Smelt and are considered a facultative anadromous species (Rosenfield and Baxter 2007). Age-0 striped bass also use open water habitats until they metamorphose in the summer (Turner and Chadwick 1972) and adults are classified as facultative anadromous species (Moyle 2002). We restricted our Striped Bass analysis to age-0 fish to minimize the potential effects of ontogenetic changes in habitat use and distribution and because older age classes are likely much less vulnerable to these sampling methods. In contrast with the other focal species, Sacramento Splittail is a littoral species (Feyrer et al. 2005, 2015) and likely not as vulnerable as the pelagic species to the sampling methods used in the three surveys.

Evaluation of System-Wide Trends

System-wide changes in the physiochemical factors that affect fish detection could potentially impose a pattern in the fish sampling data and obfuscate true trends or suggest false trends. To evaluate system-wide changes through time, we used linear mixed models to relate physiochemical measurements to year sampled. We allowed the relationship between year and each physiochemical measurement to vary among stations by including a randomly varying slope. We calculated 95% confidence intervals for the fixed effects and interpreted these as the average change in the covariate variable per year. All models were fit using R package lme4 (Bates et al. 2017).

Fish Distribution and Abundance Modeling

We considered a variety of population estimators for modeling the abundance and distribution of unmarked fishes, including N-mixture models (Royle 2004) and occupancy models (McKenzie et al. 2006). We chose occupancy models because we believed they were more robust than N-mixture estimators in the face of unexplained variation and low capture probabilities (<0.3; McIntyre et al., 2012; Couturier et al., 2013; Yamaura, 2013). Furthermore, pseudo

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CV values (Duarte et al. 2018) calculated for each species and survey were greater than 3 indicating that N-mixture models were inappropriate. However, we also wanted to evaluate trends and biases in fish abundance. Thus, we chose to use multistate occupancy models (MacKenzie et al. 2009) to evaluate the relationship between habitat and water quality characteristics, tide and sampling conditions, effort, and method on the distribution, abundance, and detection of fishes. The multistate occupancy model differs from a more familiar two-state (i.e., presence and absence) occupancy model in that the presence and detection of three or more states are estimated simultaneously. The fundamental assumption of occupancy models is that the populations are closed. That is, the occupancy state cannot change between replicate samples. This means that fish could enter and leave a station so long as the occupancy state did not change. Here, we considered three states: absent, present, and present and abundant. Thus, our model estimated the following parameters:

$\Psi^1_{i,j,k}$= probability that a station is occupied during a survey regardless of abundance;

$\Psi^2_{i,j,k}$= probability that the station is occupied by a large number of fish (abundant), given that the station is occupied during a survey;

$p^1_{i,j,k,t}$= probability that a species is detected at a station on tow t, given that true state is present, but not abundant;

$p^2_{i,j,k,t}$= probability that a species is detected at station on tow t, given that true state is present *and* abundant; and

$\delta_{i,j,k,t}$= probability that evidence of the abundant state is collected at a station on tow t, given that true state is present *and* abundant,

where i, j, and k denote survey, station, and year, respectively. Given the conditional nature of the probabilities, the probability that a station contains a large number of fish (i.e., the abundant state is present) is $\Psi^1 * \Psi^2$ and the probability of detecting the abundant state is $p^2 * \delta$. We defined the abundant state using the raw catch data for each survey from the period 1995–2015. Using the maximum catch at a station for each survey and year, we calculated the 80th percentile of the catch for each species and defined the abundant state as catches that exceeded the 80th percentile. If the 80th percentile was less than or equal to one fish, we set the threshold defining the abundant state at two fish. Although the number of animals caught that is used to define the abundant state is arbitrary (MacKenzie et al. 2017), a simulation of various cutoff values across a range of known abundances and capture probabilities used in Duarte et al. (2018) indicated that this cutoff rule resulted in the lowest misclassification error (i.e., mistaking low abundant for high abundant; J. Peterson unpublished data).

Each parameter in the multistate occupancy model can be estimated as a logit-linear function of covariates:

$$\eta_{i,j,k} = \beta_0 + \beta_1 X_{1,i,j,k} + \ldots \beta_Q X_{Q,i,j,k}, \qquad (1)$$

where η is the log-odds of the response (e.g., occupancy), and $X_{1i} \ldots X_{Qi}$ are the Q (total) predictor variables for survey (i), station (j), and year (k), β_0 is the intercept, $\beta_1 \ldots \beta_Q$ are the coefficients. The detection models included an additional subscript to denote each tow (t).

Multiple surveys were conducted at a station or within a year and samples collected at a station or within a year were likely to be more similar to one another and thus, statistically dependent. Some of the differences between years and stations can be accounted for using covariates, but any unexplained variation has the potential to induce lack of fit, biased standard errors, and flawed inferences. In addition, the variance in model parameters that remains unexplained may vary among stations or years. To account for the dependence, we examined the relations among habitat and water quality characteristics, tide, sampling conditions, effort, and method on species-specific distribution and abundance by incorporating random effects (Royle and Dorazio 2008):

$$\eta_{i,j,k} = \beta_{0,j,k} + \beta_{1,j,k} X_{1,i,j,k} + \ldots \beta_{Q,j,k} X_{Q,i,j,k}, \qquad (2)$$

where the variables are defined above. The intercept and coefficients (i.e., the β_Q) can be treated as fixed, in which their value is assumed equal across stations and years or alternatively, as randomly varying in which their values differ among stations and years. Unexplained variation in occupancy and abundant states among stations and years was incorporated by including a randomly varying intercept:

$$\beta_{0,j,k} = \gamma_{0,0} + u_{0,k} + u_{0,j,k}, \quad (3)$$

where $\gamma_{0,0}$ is the grand mean intercept, the u are random effects that are normally distributed with mean of zero and variance τ corresponding to station (j), year (k), and station by year interaction ($j:k$). The year random effect $\tau_{0,k}$ is a temporal component that represents a synchronous change through time at all locations, across years. The station random effect, $\tau_{0,j}$ is a spatial component that represents predictable unevenness between locations, independent of year. The spatialtemporal interaction component, $\tau_{0,j:k}$ represents a change in the magnitude of the difference between locations from year to year. We also evaluated the incorporation of random effects for survey nested within year in the occupancy and detection models during preliminary model fitting, but there was no support for these effects (see "Model Selection").

To accommodate a multistate occupancy model structure that included random effects, we used Markov Chain Monte Carlo (MCMC) in JAGS (Plummer 2003) implemented in R statistical software package *jagsUI* (Kellner 2016). We fitted all candidate models with 3 chains running 150,000 iterations, 100,000 adaptation samples, 25,000 burn-in samples, and minimally informative priors (Gelman et al. 2008). We assessed the convergence of each model with the Brooks and Gelman diagnostic ($\hat{R}$) (Brooks and Gelman 1998), and was assumed when $\hat{R} < 1.05$. In addition, we used parameter history and autocorrelation plots to confirm our assessment of convergence. The JAGS code for fitting the base model can be found in Appendix A.

Model Selection

Before we fit the model, we binary coded (0, 1) all categorical predictors: high, low, and flood tides were coded as 1 with ebb tide as the baseline (0); waves- waves with no whitecaps, waves with whitecaps were coded as 1 and calm as the baseline; and tow direction- against the current were coded as 1 and with or no current as 0. We also binary coded the otter trawl in the Bay Study as 1 and 0 for the midwater trawl and assigned a tow number for each station and survey to allow us to evaluate the potential effect of previously executed tows on fish detection. To evaluate the relationship between detection and fish length, we calculated the mean total length of fish that were captured on each survey. If zero fish were collected during a survey at all stations, mean length was linearly interpolated from the two nearest (in time) surveys that captured fish. All continuous predictor variables were standardized with a mean of zero and standard deviation of one. Missing continuous predictor values occurred in < 10% of samples and were assigned the mean of all observed values and missing categorical predictors were assigned a zero.

Our modeling objective was to obtain the best approximating multistate occupancy model, given the predictor variables that were available. Our first step was to determine the best approximating variance structure for the random effects. We initially fit global Ψ^1 and Ψ^2 models that contained uncorrelated predictors that represented day-of-year and time-of-day, water depth, visibility, temperature, conductivity (Table 1), tide, and surface conditions (waves), and assuming constant (intercept only) detection probabilities. We then included random effects for Ψ^1 and Ψ^2 representing station, year, and station by year interaction. Random effects were retained if their inclusion lowered the mean deviance by more than 2.

Given the best approximating variance structure, we used a stepwise procedure for selecting covariates for each model parameter. We began by fitting Ψ^1 and systematically including pairwise uncorrelated predictor variables (Pearson $|r| < 0.7$ following Moore and McCabe 1993). Predictor variables were retained when the mean deviance decreased by more than two and the 95% credible intervals of the coefficient estimate did not contain zero. In addition, we retained predictors with the 95% credible intervals containing zero when the change in deviance exceeded four. The fit of strongly correlated predictor variables, such as top and bottom conductivity, were evaluated individually and the predictor that decreased deviance the most was retained provided all model selection criteria were met. The process was repeated for Ψ^2, p^1, p^2, and δ, respectively. However,

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Table 1 Mean, standard deviation (in parentheses), and upper, lower 95th percentile (second line) of variables used in the multistate occupancy models of fish abundance, distribution, and detection

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Day-of-year [a]	132.9 (34.48) 74, 198	197.3 (23.27) 156, 238	183 (102.03) 8, 342
Time-of-day (h) [a]	10.5 (2.40) 7, 15	10.1 (2.25) 6, 15	10.2 (2.18) 7, 15
Time since sunrise (h)	4.4 (2.40) 1, 9	4.1 (2.12) 1, 8	3.6 (2.18) 0, 8
Depth (m) [a]	7.2 (3.57) 2, 15	8.0 (3.59) 2, 15	8.9 (5.11) 3, 20
Secchi depth (cm) [a]	53.7 (33.18) 15, 144	60.5 (36.4) 18, 159	74.3 (42.33) 15, 180
Surface turbidity (NTU)		23.4 (14.58) 4, 57	
Surface water temperature (°C) [a]	17.9 (3) 12, 24	21.6 (1.83) 19, 26	15.9 (3.80) 9, 22
Average water temperature (°C)			15.8 (3.75) 9, 22
Bottom water temperature (°C)			15.8 (3.71) 9, 22
Surface conductivity (µs cm^{-1}) [a]	4130.2 (7329.35) 115, 27050	5246.4 (8180.12) 122, 30541	24695.9 (18387.28) 246, 48551
Average conductivity (µs cm^{-1})			25683.8 (18505.17) 246, 48730
Bottom conductivity (µs cm^{-1})	4548.5 (7822.60) 117, 27776	5844.5 (8474.12) 124, 31754	26385.6 (18586.66) 246, 48913
Surface salinity (ppt)			15.6 (11.95) 0, 32
Average salinity (ppt)			16.3 (12.04) 0, 32
Bottom salinity (ppt)			16.7 (12.10) 0, 32
X2 (km)*	69.9 (11.48) 50, 93	80.3 (8.41) 59, 95	75.7 (12.46) 49, 93
Tow duration (min)	9.8 (1.06) 5, 10	10 (1.00) 10,11	8.14 (3.49) 4,12
Tow volume (m^3)	896.9 (122.59) 515, 1071	822.2 (105.74) 658, 1044	
Tow distance (km)			0.6 (0.14) 0, 1

a. Indicates variables that were in the global ψ^1 and ψ^2 models.

candidate predictors for the detection parameters included measures of sampling effort: tow duration, distance and volume (Table 1), tow number, and sample order. We also modeled p^2 as equal to p^1 but included an additional predictor, abundant, to account for the potential effect of a greater number of fish on species detection. Once the main effects were selected for all multistate occupancy model parameters, we evaluated all two-way interactions and quadratic terms for these parameters, which were retained in the models if the model selection criteria were met. For models that contained X2 and day-of-year, we evaluated evidence that these relationships varied by station and year, respectively, by fitting models with parameters (slopes) that varied randomly among stations and years, respectively. These randomly varying effects were retained in the model if their inclusion decreased mean deviance by more than two.

All inferences were based on the final best-fitting species and study-specific models. To facilitate interpretation, we calculated scaled odds ratios for selected parameter estimates (Hosmer and Lemeshow 2000). Because we had standardized continuous predictor variable data before we fit the model, the odds ratios should be interpreted as changes associated with a 1 standard deviation change in the corresponding predictor variable. To allow interpretation of the relative magnitude of random effects, we calculated median odds ratios for the year and station random effects following Larsen et al. (2000). Median odds ratios should be interpreted as the odds ratio between a randomly chosen station (or year) with highest probability of occupancy/abundant and a randomly chosen station (or year) with the lowest probability, assuming the stations were identical with respect to the covariates in the model.

The probability of detecting a fish depends on the probability of capturing (q) at least one fish, given N fish are present (with $N > 0$). Assuming independence among fish (but see Bayley and Peterson 2002), this can be expressed as:

$$p = 1 - (1 - q)^N, \quad (4)$$

where p is the probability of detection. We can use the above equation and the estimates of species detection probabilities from the multistate occupancy model to estimate the relative differences in true fish abundance as:

$$x_N = \frac{\log(1-p^2)}{\log(1-p^1)}, \tag{5}$$

where log is the natural logarithm, p^1 and p^2 are the average, species and study-specific probabilities of detection estimated with the best fitting multistate occupancy models, and x_N estimates the ratio of the abundance, on average, of a species in the abundant and non-abundant states.

The spatial-temporal random effects interaction component could potentially reflect large-scale changes in the distribution and abundance of fish through time that are unrelated to the covariates in the models. To identify some of these changes, we used linear regression to evaluate the relationship between the station and year interaction random effects at each station, survey, and species (i.e., $u_{0,j:k}$ in Equation 3). Stations with precise slopes (i.e., 95% confidence limits that did not contain zero) and with parameter estimates that were greater (absolute value) than 0.02 were identified as stations with significant trends in occupancy, unrelated to the model covariates. This change equates to estimated occupancy and abundance states in 2015 that were at least 1.5 times, on average, more or less likely to occur at a site since 1995. For example, this would equate to a station that was occupied on average 50% of the time in 1995 to being occupied 75% of the time in 2015. Models were fit using the *lmList* function in the R package *lme4* (Bates et al. 2017).

One of our objectives was to determine if the incomplete detection of fish resulted in biased estimates of fish distribution and abundance and affected perceived trends in occupancy and abundance based on indices calculated using raw (unadjusted) catch data. We evaluated the latter for each species and study by estimating the average proportion of stations that were occupied during a survey each year regardless of abundance and occupied by the abundant state with the best fitting model. The same two metrics also were estimated for each year using the raw catch data (henceforth, naïve estimates). Pearson correlations were calculated between the model and naïve estimates. We also estimated average percent bias in the naïve occupancy and abundant state occupancy as the naïve estimate minus the corresponding model estimate, divided by the model estimate.

RESULTS

There was very little spatial overlap among all three surveys with a single station in common (Figure 1) because of the purposeful design of the surveys. The greatest spatial overlap was between the 20 mm Survey stations and Summer Townet Survey that had 36 stations in common. By design, there also was minor temporal overlap between those two surveys (Table 1). The degree of spatial and temporal overlap affected the range of conditions observed during sampling. Specific conductance and Secchi depth were generally lowest for the 20 mm Survey and greatest for the Bay Study, though there was a high degree of overlap among all surveys (Table 1). Water temperatures were also greatest for the Summer Townet Survey, and there was less overlap in temperatures among surveys.

There were system-wide changes for most of the physiochemical characteristics measured during surveys (Table 2). Most notably was Secchi depth which increased, on average, more than 1 cm per year for the 20 mm Survey and Summer Townet Survey. There also were relatively large increases in X2, specific conductance, and salinity and smaller, but significant, decreases in temperature across all surveys (Table 2).

Detection

The best fitting multistate occupancy models indicated a few commonalities for the detection models among species and gear. Fish abundance (abundant) was included in all species detection models (Table 3) and was among the greatest factor affecting species detection (Figure 2). Most species were more than 5 times more likely to be detected when the station was occupied by the abundant state. The next most common factor influencing species detection was Secchi depth, which was strongly and negatively related to detection across most methods and species with the exception of the otter trawl, which was smaller but positively related to species detection for Longfin Smelt, Striped Bass, and Sacramento Splittail (Figure 2). The Bay Study

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Table 2 Average annual change and 95% confidence intervals (in parentheses) for physiochemical measurements collected during three long-term surveys in the San Francisco Estuary, 1995–2015

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Depth	0.04 (-0.028, 0.108)	0.033 (-0.037, 0.102)	0.046 (0.024, 0.068)
Secchi depth	1.151 (0.714, 1.587)	1.799 (1.259, 2.34)	0.799 (0.487, 1.111)
Surface turbidity		-0.124 (-0.465, 0.217)	
Surface water temperature	-0.071 (-0.091, -0.052)	-0.002 (-0.016, 0.011)	-0.051 (-0.064, -0.038)
Bottom water temperature			-0.047 (-0.066, -0.028)
Surface conductivity	201.063 (138.694, 263.432)	226.81 (148.835, 304.785)	286.155 (241.976, 330.334)
Bottom conductivity	206.847 (145.541, 268.152)	159.776 (66.055, 253.496)	240.014 (198.583, 281.445)
Surface salinity			0.185 (0.156, 0.213)
Bottom salinity			0.153 (0.126, 0.18)
X2	0.816 (0.774, 0.858)	1.648 (0.992, 2.303)	0.586 (0.546, 0.627)

trawl also was more efficient at detecting species than midwater trawl for the same three species (Figure 2). Interestingly, sampling effort (tow volume, distance, duration) was only weakly related to species detection. The best fitting abundant state detection models were similar to the best species detection models with a few notable exceptions (Table 4). The otter trawl was less likely to detect the abundant state of Delta Smelt and Longfin Smelt, but much more likely to detect Striped Bass and Sacramento Splittail (Figure 3). Secchi depth also was negatively related to detection of the abundant state for most species and methods with the exception of Striped Bass and Sacramento Splittail (Figure 3).

A comparison of the average detection probabilities across species and methods indicated the probability of detecting the species and the abundant state was greatest for Longfin Smelt and Striped Bass collected with oblique tows for the 20 mm Survey (Table 5). For example, the probability of detecting Longfin Smelt presence with the 20 mm Survey, given the species was not abundant, averaged 60%, whereas the probability of detecting the abundant state when it was present averaged 86%. In contrast, the midwater trawl used for the Bay Study was the worst performing gear for detecting species (low abundance) and the abundant state across species and ranged from 1–6% for detecting the non-abundant state and 5–35% for detecting the abundant state (Table 5). The ratio of abundant to non-abundant state fish abundances estimated using p^1 and p^2 suggested that the abundance of fish in the abundant state were, on average, 6 times greater than the non-abundant state across species and surveys (Table 5). The greatest estimated differences were for Delta Smelt collected during the 20 mm Survey with fish abundance in the abundant state more than 10 times greater than the non-abundant state.

The evaluation of system-wide changes in physiochemical characteristics indicated that Secchi depth was increasing through time, which suggests that detection may have decreased through time. Plots of average estimated detection probabilities by year suggests that detection decreased through time for all four species sampled during the Summer Townet Survey, but the magnitude varied among species (Figure 4).

Table 3 Parameter estimates, standard deviation (in parentheses) and upper, lower 95% credible intervals (second line) of detection probability (p^1, p^2) from best fitting multistate occupancy model for each species and long-term survey

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Delta Smelt			
Intercept	-1.976 (0.067) -2.108, -1.849	-2.566 (0.217) -3.013, -2.150	-2.838 (0.198) -3.220, -2.446
Time since sunrise	-0.102 (0.034) -0.169, -0.035	0.108 (0.050) 0.010, 0.206	
Depth		0.104 (0.046) 0.015, 0.195	0.168 (0.084) 0.001, 0.391
Secchi depth	-0.689 (0.049) -0.785, -0.594	-2.197 (0.146) -2.483, -1.913	-1.002 (0.125) -1.251, -0.759
Abundant (p^2) detect	3.001 (0.076) 2.855, 3.149	1.489 (0.187) 1.135, 1.875	2.230 (0.223) 1.797, 2.683
Tow duration	0.167 (0.037) 0.096, 0.239		
Tow volume		-0.147 (0.048) -0.242, -0.055	
Mean fish length	-0.206 (0.036) -0.276, -0.134		
Otter trawl			-1.557 (0.155) -1.862, -1.259
Otter trawl × Secchi depth			0.273 (0.132) 0.016, 0.621
Otter trawl × Depth			-0.319 (0.134) -0.584, -0.060
Longfin Smelt			
Intercept	0.396 (0.037) 0.323, 0.469	-2.256 (0.230) -2.705, -1.809	-3.690 (0.132) -3.950, -3.439
Depth			0.457 (0.050) 0.360, 0.553
Secchi depth		-1.316 (0.175) -1.657, -0.975	-1.727 (0.066) -1.856, -1.597
Abundant detect	3.839 (0.148) 3.558, 4.136	1.973 (0.207) 1.573, 2.385	2.376 (0.108) 2.159, 2.580
Tow duration	0.173 (0.050) 0.075, 0.271		
Tow volume	-0.122 (0.046) -0.211, -0.031		
Tow distance			0.508 (0.058) 0.389, 0.619
High tide			0.795 (0.163) 0.476, 1.118
Mean fish length	-0.163 (0.031) -0.222, -0.102		
Otter trawl			2.038 (0.124) 1.793, 2.270
Otter trawl × Secchi depth			2.017 (0.074) 1.869, 2.159
Otter trawl × Depth			-0.586 (0.057) -0.696, -0.475
Otter trawl × High tide			-0.659 (0.193) -1.040, -0.286

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Striped Bass			
Intercept	0.646 (0.052) 0.544, 0.751	-1.241 (0.085) -1.410, -1.075	-2.857 (0.147) -3.150, -2.568
Time since sunrise		-0.206 (0.039) -0.283, -0.131	
Depth	0.152 (0.029) 0.095, 0.208		0.507 (0.060) 0.390, 0.623
Secchi depth		-0.980 (0.077) -1.132, -0.832	-1.545 (0.065) -1.675, -1.420
Abundant detect	3.908 (0.172) 3.585, 4.256	2.508 (0.103) 2.306, 2.709	1.801 (0.117) 1.569, 2.026
Tow distance			0.258 (0.056) 0.150, 0.369
Mean fish length	-0.484 (0.048) -0.579, -0.392		
Otter trawl			1.725 (0.124) 1.481, 1.973
Otter trawl × Secchi depth			2.081 (0.077) 1.933, 2.234
Otter trawl × Depth			-1.676 (0.063) -1.801, -1.554
Sacramento Splittail			
Intercept	-1.742 (0.257) -2.233, -1.227	-2.653 (0.300) -3.284, -2.088	-4.559 (0.357) -5.299, -3.903
Time since sunrise	0.252 (0.129) 0.006, 0.509		
Secchi depth		-1.064 (0.188) -1.433, -0.697	-2.441 (0.216) -2.873, -2.028
Abundant detect	2.389 (0.206) 1.984, 2.798	1.676 (0.298) 1.137, 2.306	1.691 (0.318) 1.071, 2.314
Otter trawl			1.122 (0.198) 0.741, 1.520
Otter trawl × Secchi depth			2.500 (0.220) 2.090, 2.953
Otter trawl × Depth			-0.859 (0.153) -1.159, -0.565

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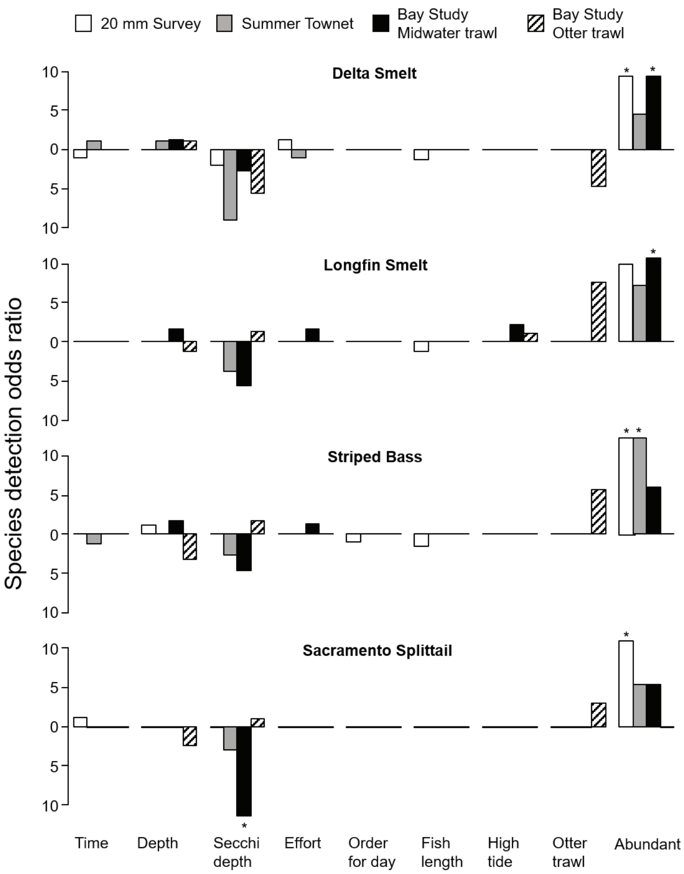

Figure 2 Estimated odds ratios for species detection probability (p^1 and p^2) from best approximating multi-state occupancy model by survey and species. Bars below the axis should be interpreted as detection is less likely, whereas bars above the axis indicate more likely. Odds ratios for continuous covariates correspond to a 1-standard deviation increase in the covariate and asterisks indicate values that exceed range plotted.

Occupancy

The best fitting species occupancy models indicated that four factors: day-of-year, water temperature, salinity or specific conductance, and X2, were consistently included in the species occupancy models across species and surveys (Table 6). Of these, salinity or specific conductance generally had the greatest effect on occupancy across species (Figure 5). However, the magnitude and direction of these effects generally differed among surveys for a species (Figure 5). For instance, Longfin Smelt occupancy was negatively related to specific conductance for the 20-mm Survey but positively related for the Summer Townet Survey and Bay Study. The effect

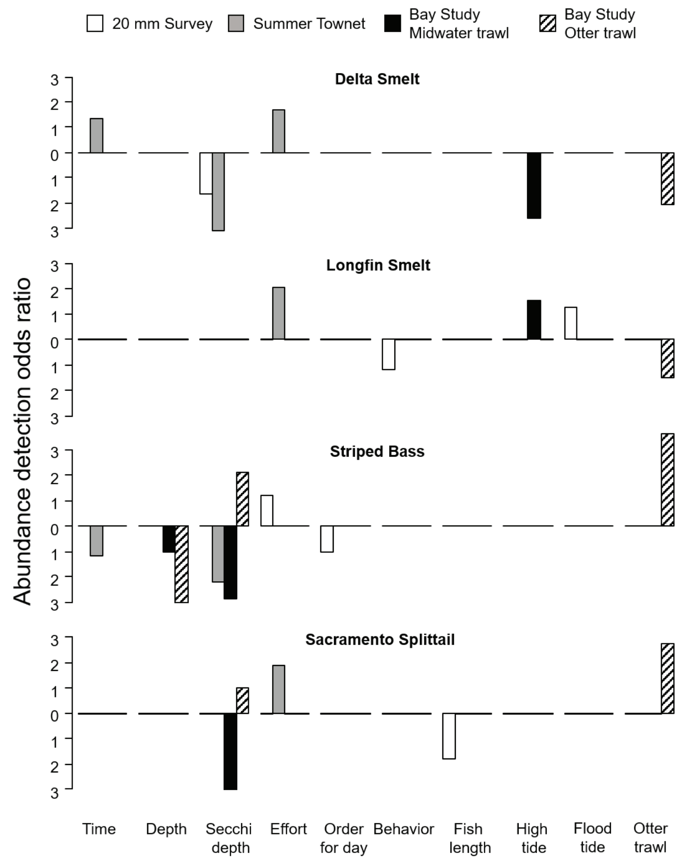

Figure 3 Estimated odds ratios for conditional abundant detection probability (d) from best approximating multi-state occupancy model by survey and species. Bars below the axis should be interpreted as detection of abundant state is less likely, whereas bars above the axis indicate more likely. Odds ratios for continuous covariates correspond to a 1-standard deviation increase in the covariate and asterisks indicate values that exceed range plotted. Behavior is estimate of effect of previous tows on detection.

of salinity and specific conductance also differed by orders of magnitude among studies for the other three species (Figure 5). Delta Smelt and Sacramento Splittail occupancy were negatively related to water temperature for the Summer Townet Survey, but positively related for the Bay Study.

The average effect of X2 on occupancy was relatively small compared to day-of-year, water temperature, and salinity or specific conductance (Figure 5). However, the effect of X2 on species occupancy varied substantially among stations for each species (Table 6). On average, the effect of X2 (on a logit

Table 4 Parameter estimates, standard deviation (in parentheses) and upper, lower 95% credible intervals (second line) of conditional abundant state detection probability (d) from best fitting multistate occupancy model for each species and long-term survey

Parameter	20-mm Survey	Summer Townet	Bay Study
Delta Smelt			
Intercept	0.908 (0.066) 0.779, 1.039	1.384 (0.217) 0.967, 1.814	0.506 (0.172) 0.190, 0.860
Time since sunrise		0.282 (0.096) 0.094, 0.472	
Secchi depth	-0.471 (0.068) -0.603, -0.338	-1.123 (0.270) -1.661, -0.586	
Tow volume		0.503 (0.106) 0.303, 0.717	
High tide			-0.948 (0.332) -1.611, -0.310
Otter trawl			-0.712 (0.224) -1.159, -0.275
Longfin Smelt			
Intercept	1.885 (0.126) 1.638, 2.133	2.410 (0.161) 2.105, 2.735	1.061 (0.093) 0.886, 1.249
Tow volume		0.714 (0.150) 0.426, 1.019	
Flood tide	0.221 (0.094) 0.037, 0.406		
High tide			0.410 (0.159) 0.105, 0.729
Tow number	-0.181 (0.053) -0.283, -0.074		
Otter trawl			-0.404 (0.094) -0.591, -0.220
Striped Bass			
Intercept	1.373 (0.075) 1.227, 1.523	0.412 (0.089) 0.239, 0.591	-1.027 (0.105) -1.229, -0.819
Time since sunrise		-0.153 (0.055) -0.262, -0.047	
Depth			-0.021 (0.082) -0.182, 0.140
Secchi depth		-0.791 (0.106) -1.001, -0.580	-1.043 (0.117) -1.270, -0.811
Tow volume	0.215 (0.048) 0.122, 0.309		
Order for day	-0.008 (0.005) -0.017, 0.001		
Otter trawl			1.290 (0.121) 1.047, 1.523
Otter trawl × Secchi depth			1.803 (0.143) 1.524, 2.084
Otter trawl × Depth			-1.418 (0.124) -1.669, -1.182
Sacramento Splittail			
Intercept	-0.004 (0.158) -0.308, 0.313	1.989 (0.308) 1.430, 2.643	-1.652 (0.392) -2.389, -0.867
Secchi depth			-1.320 (0.347) -1.995, -0.629
Tow volume		0.635 (0.249) 0.189, 1.159	
Mean fish length	-0.595 (0.293) -1.187, -0.028		
Otter trawl			1.018 (0.429) 0.149, 1.834
Otter trawl × Secchi depth			1.338 (0.411) 0.515, 2.115

the X2 effect among stations occurring for Longfin Smelt (Table 6).

The best fitting species occupancy models also contained random effects corresponding to station, year, and station by year interaction. Median odds ratios suggested that the magnitude of these effects were generally greater than the effects of physiochemical characteristics (Figure 5). There was no clear or consistent pattern in the relative magnitude of spatial and temporal variation that was not accounted for by the predictor variables across species. Spatial variation greatly exceeded temporal variation for Longfin Smelt across surveys, but relative magnitude of spatial and temporal variation differed among surveys for the other three species (Figure 5). The relative magnitude of the station by year random effect also suggested a systematic shift in the distribution of species at stations through time.

year, salinity or specific conductance, and X2 having among the greatest effects on the presence of the abundant state (Table 7). The abundance occupancy models also contained randomly varying X2 that was most variable for Delta Smelt as estimated for the 20-mm Survey and Bay Study. The median odds ratios also suggested that spatial and temporal factors unaccounted for by the predictors had a substantial effect on the abundant state occupancy (Figure 6).

The evaluation of systematic changes in distribution and abundance of the four fish species that was unrelated to the covariates included in the analysis revealed that all species had a greater number of stations where occupancy or abundance decreased

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Table 5 Estimated multi-state detection probabilities under average sampling conditions, the ratio of abundant to non-abundant state fish abundances (x_N), the correlation between estimated and naïve occupancy and abundant (in parentheses), and the estimated percent bias of naïve occupancy and abundant state (in parentheses) relative to model estimated values. Otter trawl estimates shown separately for the Bay Study. The conditional state detection estimates the probability that the abundant state is collected at a station during a tow given that true population state is present and abundant.

Study / Species	p^1	p^2	δ^*p^2	p^1(otter)	p^2(otter)	δ^*p^2(otter)	x_N	Pearson r	Bias (%)
20-mm Survey									
Delta Smelt	0.12	0.74	0.52				10.26	0.85 (0.99)	-46.6 (-6.7)
Longfin Smelt	0.60	0.99	0.86				4.67	0.99 (0.99)	-1.2 (-0.1)
Striped Bass	0.66	0.99	0.79				4.28	0.98 (0.99)	-2.5 (-1.0)
Sacramento Splittail	0.15	0.66	0.33				6.62	0.95 (0.99)	-24.5 (-24.4)
Summer Townet Survey									
Delta Smelt	0.07	0.25	0.20				3.96	0.98 (0.97)	-11.3 (-13.5)
Longfin Smelt	0.09	0.43	0.39				5.64	0.98 (0.99)	-9.6 (-3.0)
Striped Bass	0.22	0.78	0.47				5.97	0.86 (0.99)	-25 (-7.7)
Sacramento Splittail	0.07	0.27	0.24				4.69	0.96 (0.99)	-34.3 (-6.3)
Bay Study									
Delta Smelt	0.06	0.35	0.22	0.01	0.10	0.05	7.64	0.67 (0.93)	-75.4 (-58.4)
Longfin Smelt	0.02	0.21	0.16	0.16	0.67	0.44	9.65	0.52 (0.96)	-45.4 (-33.3)
Striped Bass	0.05	0.26	0.07	0.24	0.66	0.37	5.34	0.63 (0.83)	-29.3 (-47.2)
Sacramento Splittail	0.01	0.05	0.01	0.03	0.15	0.05	5.30	0.87 (0.96)	-71.3 (-78.7)

through time with Longfin Smelt exhibiting decreases in the greatest number of stations (26) and Delta Smelt the fewest (19). The distribution and abundance of Delta Smelt appeared to contract in the Sacramento Deep Water Ship Channel and San Pablo and Suisun bays and increase in the North Delta sloughs (Figure 7). Longfin Smelt distribution appeared to contract to areas in Suisun, Honker, and South bays and around Liberty Island. Striped Bass exhibited a more complicated pattern with decreases generally occurring in the western portions of the estuary and increases in the eastern portions (Figure 7). Sacramento Splittail also exhibited a more complicated pattern with decreases in the western portion of the survey areas.

The trends in species occupancy and the abundant state as estimated with the best-fitting multistate occupancy model and the naïve estimates indicated decreases in the average proportion of stations occupied through time (Figures 8–11). For instance, Delta Smelt naïve and estimated occupancy indicated decreasing trends through time, across surveys (Figure 8). However, the estimated rate of decrease varied among surveys. Pearson correlations between average naïve and estimated occupancy rates paired by year indicated the trends were strongly correlated (Table 5). The strongest correlations were for the abundant state (average correlation across species and surveys 0.97) and the weakest were for species occupancy as estimated with the Bay Study survey data (average correlation across species and surveys 0.68). The relative biases in proportion of stations occupied by the species and the abundant state indicated that the naïve estimates substantially underestimated occupancy, with underestimates averaging across species and surveys by 31% and 23% for species presence and the abundant state presence, respectively (Table 5). Estimated occupancy rates by year, survey, and species can be found in Appendix B.

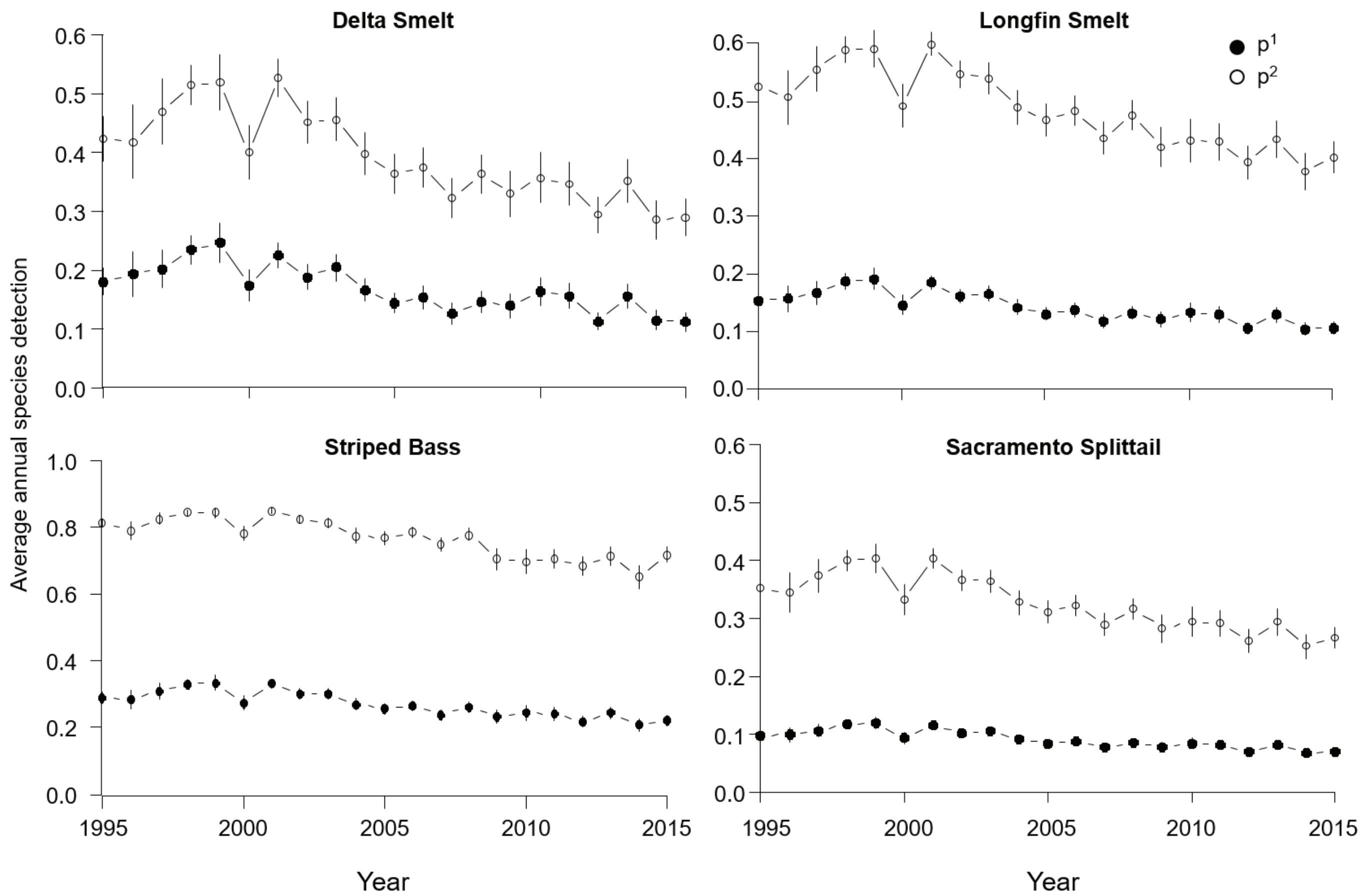

Figure 4 Average and 95th percentiles (bars) for estimated species detection probabilities for the Summer Townet Survey by year and species

DISCUSSION

Incomplete detection is the norm when conducting surveys of wild animals and the modeling results reflect this pattern with estimated detection probabilities for all four species and surveys less than 100%. The occupancy model detection probabilities depend on the species being present within the station. Thus, fish could go undetected in a tow because they were not in the tow path or moved out of the tow path. The model could not distinguish which of these mechanisms was responsible for incomplete detection. However, previous studies have found that fish move out of sample units in response to the sound and presence of research vessels (De Robertis and Handegard 2013), the presence of towed cameras (Rooker et al. 1997; Stoner et al. 2007; King et al. 2018), tow cables (Somerton et al. 2017), and towed nets (e.g., Handegard et al. 2003; Kaartvedt et al. 2012; Bryan et al. 2014; Kresimir et al. 2015). The ability to move away from towed sample gear is positively related to fish body size (Barkley 1972), which may partially explain the high detection probabilities for low abundance state of Longfin Smelt and Striped Bass for the 20-mm Survey. Fish movement out of the tow path would likely violate assumptions of perfect detection within the tow path, negatively biasing raw catch data and abundance indices calculated with the data. Clearly, there is need to evaluate the response of fish to the sample gear used in the long-term studies in the estuary.

The fundamental assumption of the multistate occupancy model is that stations were closed with respect to the occupancy state. That is, if the species was in the abundant state during the first tow it should remain in the abundant state during subsequent tows within a primary sampling period. This means that individual fish can enter and leave a station, so long as the state did not change

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Table 6 Parameter estimates, standard deviation (in parentheses) and upper, lower 95% credible intervals (below) of species occupancy (Ψ^1) from best fitting multistate occupancy model for each species and long-term survey. Italics indicate random effects that are expressed as standard deviations.

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Delta Smelt			
Intercept	0.404 (0.370) -0.326, 1.136	-1.413 (0.573) -2.549, -0.279	-3.569 (0.450) -4.476, -2.723
Day-of-year	3.680 (0.268) 3.208, 4.268	-0.227 (0.111) -0.448, -0.013	
Surface water temperature		-0.449 (0.163) -0.769, -0.137	
Average water temperature			0.567 (0.232) 0.167, 1.079
Surface conductivity		-1.092 (0.256) -1.612, -0.603	
Bottom conductivity	-3.540 (0.311) -4.219, -2.981		
Average salinity			-4.218 (0.483) -5.147, -3.222
X2		-0.259 (0.191) -0.646, 0.105	1.148 (0.266) 0.609, 1.641
$(\text{Day-of-year})^2$	0.259 (0.130) 0.010, 0.542		
$(\text{Surface water temperature})^2$		-0.280 (0.113) -0.510, -0.065	
Average salinity × average water temperature			0.764 (0.263) 0.280, 1.312
Surface conductivity × Day-of-year		0.627 (0.118) 0.401, 0.862	
X2		0.190 (0.150) 0.007, 0.553	0.410 (0.230) 0.071, 0.957
Station	1.289 (0.233) 0.886, 1.793	3.033 (0.518) 2.175, 4.206	0.696 (0.306) 0.127, 1.393
Year	1.218 (0.258) 0.802, 1.820	1.797 (0.384) 1.192, 2.666	1.203 (0.330) 0.659, 1.959
Year × Station	1.454 (0.211) 1.064, 1.867	1.297 (0.200) 0.912, 1.715	0.341 (0.204) 0.062, 0.788
Longfin Smelt			
Intercept	-0.416 (0.601) -1.591, 0.756	-2.998 (0.570) -4.126, -1.897	0.851 (0.484) -0.124, 1.742
Day-of-year	-1.453 (0.120) -1.690, -1.222	-0.881 (0.122) -1.123, -0.646	
Depth	0.382 (0.136) 0.120, 0.650	0.363 (0.154) 0.054, 0.672	
Secchi depth	-0.419 (0.086) -0.590, -0.251		
Surface water temperature	-0.297 (0.111) -0.509, -0.079	-0.755 (0.163) -1.081, -0.440	
Bottom water temperature			-2.232 (0.182) -2.615, -1.903
Bottom conductivity	-1.391 (0.150) -1.694, -1.105	0.302 (0.139) 0.290, 0.575	
Bottom salinity			1.315 (0.338) 0.614, 1.939
X2		-0.076 (0.237) -0.537, 0.395	-0.334 (0.314) -0.974, 0.266
Depth × Secchi depth	0.141 (0.073) 0.001, 0.290		
X2		0.690 (0.181) 0.383, 1.083	1.575 (0.263) 1.118, 2.150
Station	3.430 (0.440) 2.679, 4.389	2.679 (0.515) 1.835, 3.854	3.008 (0.394) 2.334, 3.861
Year	1.976 (0.356) 1.413, 2.813	1.904 (0.388) 1.299, 2.790	1.022 (0.221) 0.672, 1.538
Year × Station	1.358 (0.104) 1.158, 1.569	0.377 (0.262) 0.022, 0.891	0.618 (0.193) 0.237, 1.010

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Striped Bass			
Intercept	0.880 (0.214) 0.463, 1.311	0.982 (0.617) -0.229, 2.222	0.992 (0.458) 0.081, 1.872
Day-of-year	2.058 (0.124) 1.816, 2.300	-1.768 (0.212) -2.199, -1.393	0.231 (0.120) 0.002, 0.471
Secchi depth	-0.567 (0.073) -0.708, -0.425		
Surface turbidity		0.366 (0.115) 0.161, 0.608	
Surface water temperature	0.257 (0.109) 0.044, 0.475	-0.526 (0.181) -0.895, -0.188	
Average water temperature			-0.701 (0.114) -0.937, -0.489
Surface conductivity	-1.951 (0.136) -2.225, -1.691	-0.946 (0.246) -1.427, -0.475	
Average salinity			-3.127 (0.407) -3.934, -2.303
X2	0.509 (0.160) 0.191, 0.821	0.493 (0.378) -0.280, 1.224	0.741 (0.212) 0.321, 1.148
(Day-of-year)^2	-0.319 (0.067) -0.450, -0.186	-0.260 (0.112) -0.486, -0.047	
Surface conductivity × Day-of-year		0.917 (0.135) 0.671, 1.194	
Surface conductivity × Surface water temperature	-0.822 (0.094) -1.007, -0.636		
X2	0.777 (0.116) 0.581, 1.032	1.129 (0.257) 0.692, 1.707	0.567 (0.203) 0.180, 0.986
Station	0.842 (0.114) 0.648, 1.090	1.856 (0.306) 1.340, 2.535	2.595 (0.464) 1.848, 3.662
Year	0.702 (0.136) 0.484, 1.013	2.431 (0.530) 1.590, 3.666	0.788 (0.197) 0.467, 1.237
Year × Station	0.426 (0.101) 0.235, 0.618	0.916 (0.290) 0.248, 1.436	0.828 (0.186) 0.471, 1.209
Sacramento Splittail			
Intercept	-2.683 (0.383) -3.449, -1.937	-2.856 (0.609) -4.029, -1.620	-3.504 (0.423) -4.329, -2.677
Day-of-year	1.950 (0.288) 1.469, 2.618	-1.008 (0.242) -1.508, -0.544	
Secchi depth	-1.215 (0.218) -1.682, -0.829		
Surface water temperature	-0.689 (0.208) -1.135, -0.323	-0.974 (0.256) -1.526, -0.515	
Average water temperature			0.293 (0.219) -0.109, 0.754
Surface conductivity	-0.564 (0.201) -0.969, -0.187	-0.799 (0.314) -1.434, -0.207	
Average salinity			-3.056 (0.351) -3.788, -2.420
X2	-0.615 (0.213) -1.065, -0.213	-0.188 (0.242) -0.602, 0.285	
(Day-of-year)^2	-0.714 (0.119) -0.972, -0.504	-0.622 (0.190) -1.029, -0.276	
Average salinity × Average water temperature			-0.537 (0.194) -0.925, -0.165
X2	0.479 (0.174) 0.150, 0.857	0.201 (0.161) 0.016, 0.659	
Station	0.802 (0.192) 0.445, 1.210	1.308 (0.270) 0.852, 1.910	1.093 (0.244) 0.675, 1.635
Year	1.285 (0.309) 0.805, 2.015	2.061 (0.530) 1.236, 3.287	1.179 (0.302) 0.689, 1.866
Year × Station	0.613 (0.407) 0.025, 1.394	0.721 (0.301) 0.227, 1.349	0.467 (0.206) 0.188, 1.014

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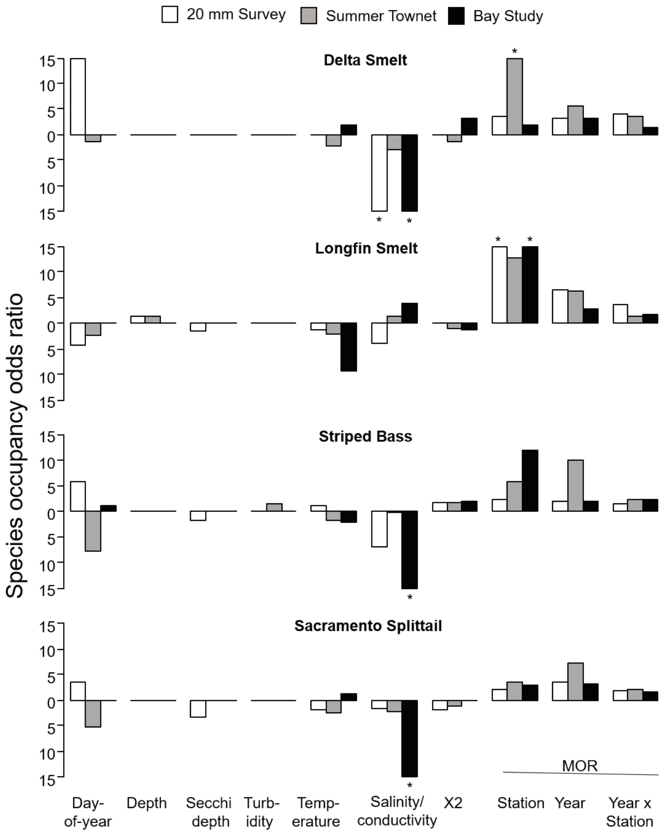

Figure 5 Estimated odds ratios and median odds ratios (MOR) for species occupancy probability (Ψ^1) from best approximating multistate occupancy model by survey and species. Bars below the axis should be interpreted as occupancy is less likely, whereas bars above the axis indicate more likely. Odds ratios for continuous covariates correspond to a 1 standard deviation increase in the covariate and asterisks indicate values that exceed range plotted.

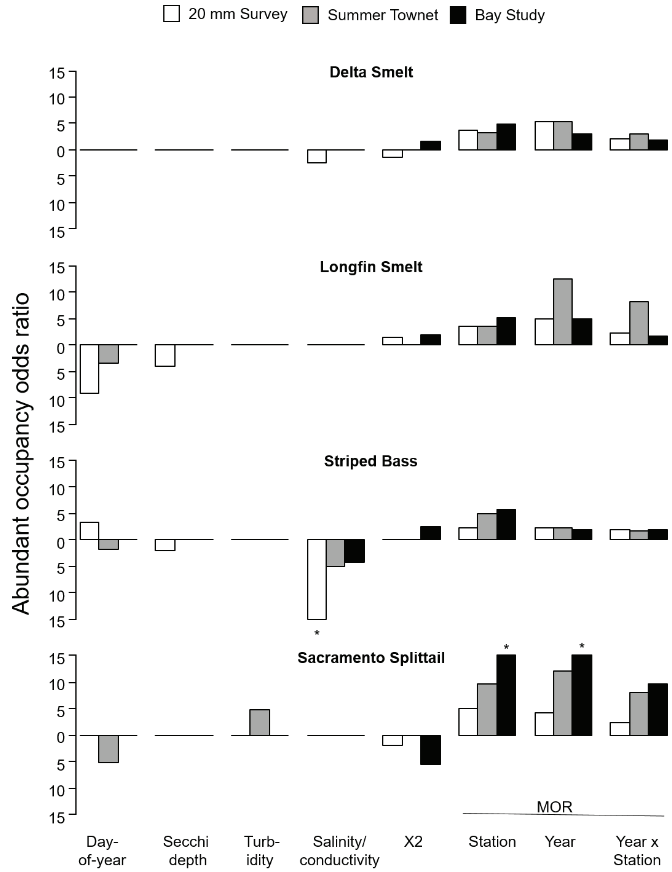

Figure 6 Estimated odds ratios and median odds ratios (MOR) for abundant occupancy probability (Ψ^2) from best approximating multistate occupancy model by survey and species. Bars below the axis should be interpreted as occupancy is less likely, whereas bars above the axis indicate more likely. Odds ratios for continuous covariates correspond to a 1-standard deviation increase in the covariate and asterisks indicate values that exceed range plotted.

within a primary sampling period. Similarly, if the station is unoccupied at the start of sampling, it was assumed that it was unoccupied during the entire primary sampling period. If the fish in a location were transported by tides into and out of stations during sampling such that the closure assumption was systematically violated, we should have observed the effect of tow, time-of-day, or tide on detection-probabilities. There was scant evidence that these factors played a role in detection. In addition, the very strong spatial effect (i.e., random effects) on occupancy and abundance suggests that there was something about the fixed stations (specific locations) unrelated to the covariates in the analysis that strongly affect fish distribution and abundance. We would not expect this strong spatial signal if fish were passive particles transported by the tides. Similarly, the very high detection rates for Longfin Smelt and Striped Bass abundant state with the 20-mm Survey also do not support the notion that the closure assumption was violated. For instance, the probability of detecting the abundant state on at least 2 of 3 trawls at a site averaged 0.99 for both species. Based on this evidence, we believe that the closure assumption was not substantially violated.

For all three surveys, the ability to detect species was strongly related to fish abundance and physiochemical characteristics of the sampling stations. These same characteristics also changed

Table 7 Parameter estimates, standard deviation (in parentheses) and upper, lower 95% credible intervals (below) of abundant state occupancy (Ψ^2) from best fitting multistate occupancy model for each species and long-term survey. Italics indicate random effects that are expressed as standard deviations.

Parameter	20-mm Survey	Summer Townet Survey	Bay Study
Delta Smelt			
Intercept	-1.508 (0.458) -2.413, -0.611	1.810 (0.553) 0.758, 2.958	-1.415 (0.529) -2.421, -0.324
Bottom conductivity	-0.856 (0.211) -1.269, -0.436		
X2	-0.221 (0.210) -0.645, 0.190		0.519 (0.335) -0.127, 1.186
X2	0.949 (0.150) 0.690, 1.278		1.186 (0.403) 0.611, 2.178
Station	1.410 (0.198) 1.078, 1.840	1.248 (0.484) 0.520, 2.400	1.648 (0.482) 0.944, 2.787
Year	1.781 (0.358) 1.215, 2.585	1.755 (0.558) 0.932, 3.087	1.154 (0.423) 0.481, 2.150
Year × Station	0.860 (0.131) 0.599, 1.117	1.170 (0.422) 0.222, 1.849	0.657 (0.329) 0.220, 1.423
Longfin Smelt			
Intercept	-1.997 (0.444) -2.887, -1.131	0.626 (0.755) -0.827, 2.161	-0.223 (0.453) -1.117, 0.668
Day-of-year	-1.637 (0.105) -1.848, -1.436	-1.225 (0.352) -2.016, -0.624	
Secchi depth	-1.369 (0.149) -1.665, -1.077		
X2	0.394 (0.219) -0.034, 0.833		0.691 (0.151) 0.403, 0.999
(Day-of-year)^2	-0.578 (0.072) -0.721, -0.441		
X2	1.006 (0.174) 0.706, 1.385		0.583 (0.135) 0.360, 0.885
Station	1.327 (0.247) 0.914, 1.878	1.299 (0.574) 0.193, 2.566	1.702 (0.262) 1.255, 2.276
Year	1.662 (0.322) 1.158, 2.418	2.655 (0.866) 1.327, 4.693	1.668 (0.316) 1.171, 2.407
Year × Station	0.885 (0.109) 0.674, 1.103	2.202 (0.603) 1.235, 3.608	0.508 (0.167) 0.199, 0.902
Striped Bass			
Intercept	-2.259 (0.269) -2.800, -1.746	-1.530 (0.333) -2.194, -0.890	-0.195 (0.413) -0.922, 0.728
Day-of-year	2.394 (0.131) 2.147, 2.661	-0.537 (0.099) -0.733, -0.344	
Secchi depth	-0.776 (0.097) -0.968, -0.586		
Surface conductivity	-3.233 (0.235) -3.706, -2.782	-1.622 (0.245) -2.107, -1.146	
Average salinity			-1.450 (0.361) -2.160, -0.706
X2			0.955 (0.201) 0.554, 1.353
(Day-of-year)^2	-1.182 (0.085) -1.351, -1.018		
X2			0.829 (0.185) 0.520, 1.235
Station	0.887 (0.136) 0.653, 1.186	1.708 (0.285) 1.231, 2.334	1.844 (0.458) 1.168, 2.985
Year	0.884 (0.173) 0.607, 1.279	0.848 (0.176) 0.567, 1.248	0.740 (0.181) 0.442, 1.156
Year × Station	0.702 (0.095) 0.520, 0.902	0.589 (0.177) 0.213, 0.929	0.773 (0.166) 0.447, 1.111
Sacramento Splittail			
Intercept	-3.406 (0.635) -4.748, -2.268	-2.144 (1.027) -4.103, -0.075	-0.392 (1.136) -2.668, 1.769
Day-of-year		-1.647 (0.705) -3.195, -0.457	
Surface turbidity		1.584 (0.690) 0.529, 3.179	
X2	-0.687 (0.426) -1.516, 0.161		-1.716 (1.040) -3.840, 0.200
X2	0.834 (0.513) 0.031, 1.957		3.023 (1.240) 0.888, 5.622
Station	1.714 (0.469) 0.966, 2.811	2.379 (0.965) 0.969, 4.734	3.494 (1.225) 1.387, 5.801
Year	1.485 (0.679) 0.444, 3.122	2.609 (1.334) 0.451, 5.554	3.838 (1.321) 0.778, 5.875
Year × Station	0.922 (0.440) 0.311, 2.079	2.186 (1.120) 0.601, 4.348	2.391 (1.425) 0.369, 5.668

systematically in the estuary across the two decades considered in this evaluation. Despite these systematic changes, temporal trends observed during this time period appeared to be largely unaffected. This was likely because of a combination of the use of replicate tows, which increased the probability of detecting a species during a survey, and the execution of multiple surveys within a year. Surveys that do not incorporate replicate samples (tows) are likely to be more susceptible to systematic changes in detection in time and space. This highlights the importance of implementing surveys with replicate samples that increase the ability to detect fish presence and can be analyzed using one or more population estimators that account for imperfect detection.

Although trends in occupancy and abundance appeared to be unbiased, the estimates based of the raw catch were systematically lower than the multistate occupancy estimates. For instance, the

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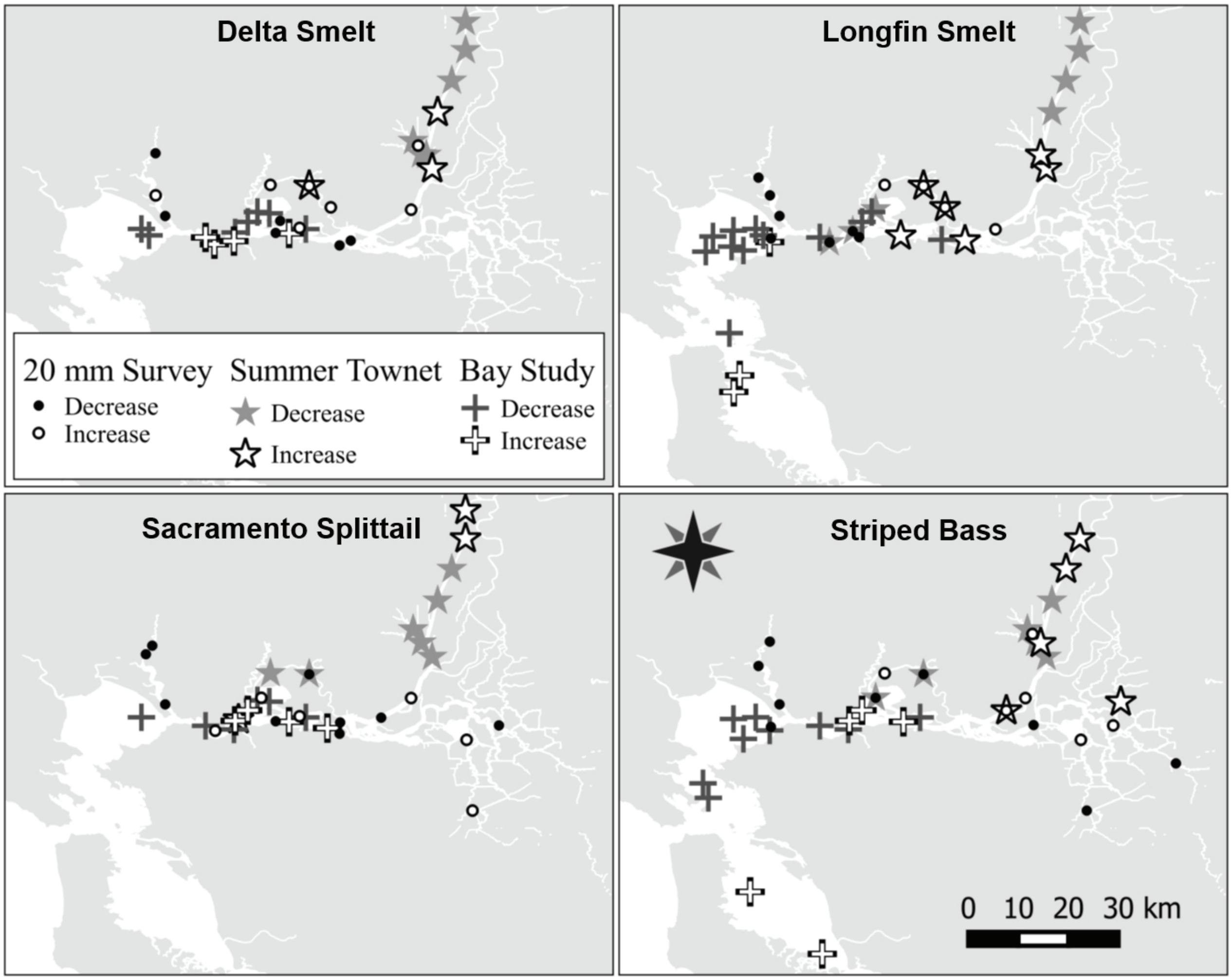

Figure 7 Survey stations that exhibit systematic increases and decreases in occupancy and abundance of the four study species from 1995–2015

ratio of naïve occupancy to estimated occupancy for Delta Smelt averaged 0.51 for the 20-mm Survey, which indicates that the tows failed to detect Delta Smelt at a station when they were actually present half the time. The biases were particularly large for the Bay Study. We believe that these larger biases were because of the fact that each replicate tow sampled different populations of fishes. Occupancy estimators assume that all the species present are available for capture with the sampling gear (MacKenzie et al. 2017). However, the midwater trawl primarily samples fish in the water column, whereas the otter trawl is sampling fish on the bottom. Thus, fish available for capture with one gear may not be available for capture with the other. The probability of detecting a species or the abundant state with single pass with each gear would have been lower resulting in significant underestimates. These differences were accounted for in the model by including a covariate for method and further highlight the importance of collecting replicate samples. Additionally, the substantial differences in detection between the two Bay Study gears suggests that a single gear may not be adequate for sampling and characterizing the fish community.

Occupancy is defined as the presence of at least one individual at a sample site or station. Once occupied, the detection of a species at a station depends on the efficiency of the method (i.e., the capture probability) and the number of animals available for capture. Thus, it was expected that the

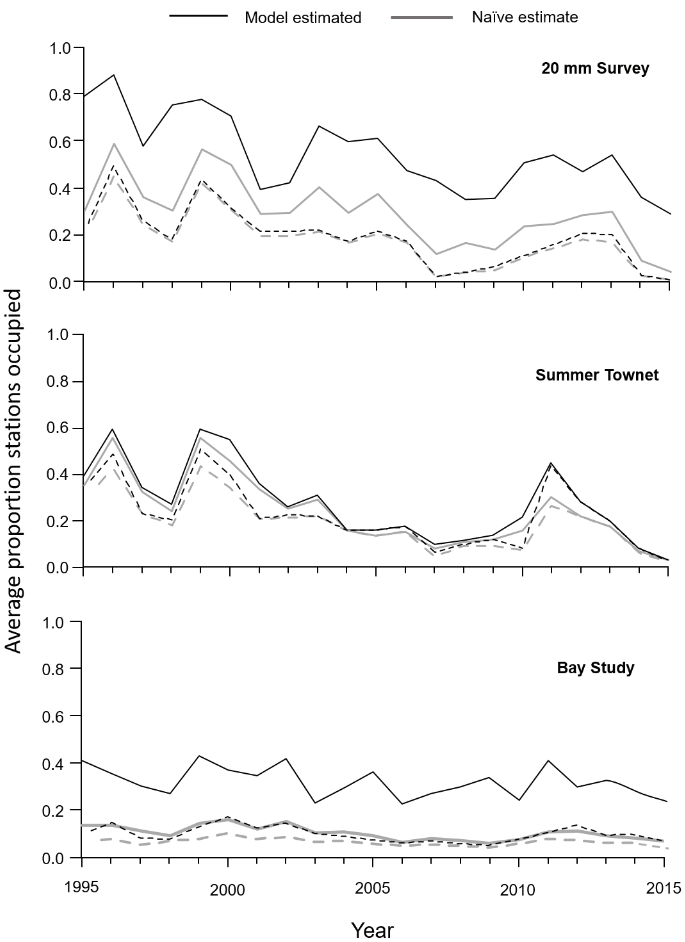

Figure 8 Annual trends in average proportion of stations occupied by Delta Smelt (solid lines) and the abundant state (broken lines) estimated using the best fitting multistate occupancy model and with the raw catch data (naïve) from 1995–2015

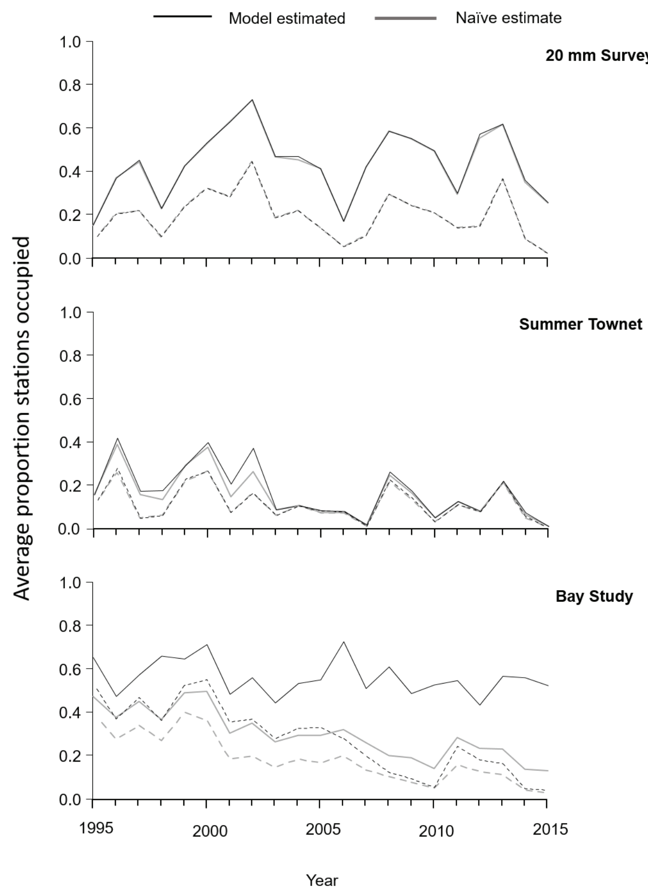

Figure 9 Annual trends in average proportion of stations occupied by Longfin Smelt (solid lines) and the abundant state (broken lines) estimated using the best fitting multistate occupancy model and with the raw catch data (naïve) from 1995–2015

probability of species detection (i.e., collecting at least 1 individual) was greatest when the abundant state was present. Similarly, 20-mm Survey detection probabilities were greater than the Summer Townet Study and Bay Study because of the greater number of small (larval) fish present in the system during sampling. This highlights the importance of understanding that these two factors interact when interpreting the detection probability models. For instance, previous studies reported on the negative relationship between Secchi depth and catch per unit effort (CPUE) for three of the four species included in this study (Sommer and Mejia 2013; Latour 2015). The relationship between Secchi depth and detection probability could represent the effects of turbidity on fish abundance. However, there was weaker evidence that the abundant state occupancy was strongly related to Secchi depth or turbidity. Previous studies have also found that water clarity is negatively related to the efficiency of seines for collecting cyprinids (Bayley and Peterson 2001; Price and Peterson 2010), presumably because of fish being able to detect and avoid the gear in clearer water. We believe that Secchi depth affects detection as a result of the combined effects of turbidity on abundance and capture probability. If true, previously reported negative relationships between CPUE and turbidity are likely positively biased because capture probability was greater under turbid conditions.

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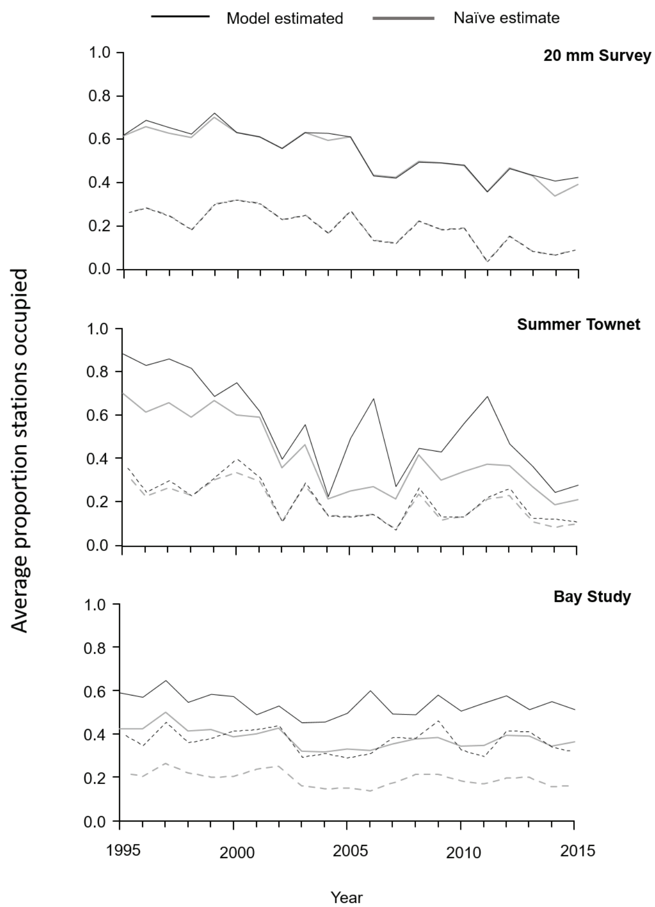

Figure 10 Annual trends in average proportion of stations occupied by Striped Bass (solid lines) and the abundant state (broken lines) estimated using the best fitting multistate occupancy model and with the raw catch data (naïve) from 1995–2015

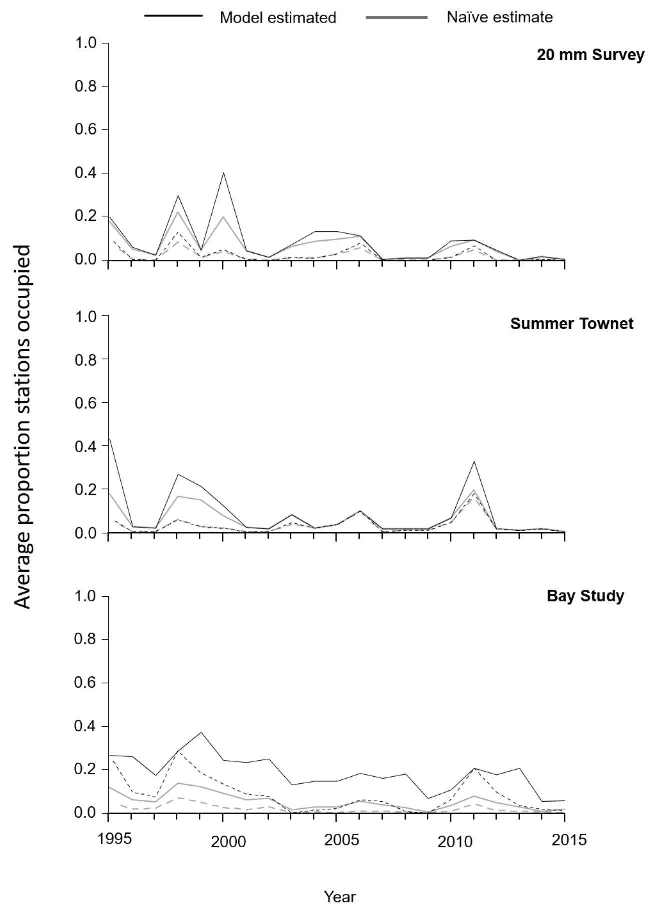

Figure 11 Annual trends in average proportion of stations occupied by Sacramento Splittail (solid lines) and the abundant state (broken lines) estimated using the best fitting multistate occupancy model and with the raw catch data (naïve) from 1995–2015

Sampling effort measured as tow duration, distance and volume, was weakly related to the probability of detection and was only consistently related to conditional detection of the abundant state for the Summer Townet Study. Greater effort during sampling should, in theory, expose a greater number of fish to capture, thereby increasing detection probability. This reasoning is presumably why fish catch data for these surveys are often expanded using the volume of water sampled (Honey et al. 2004). One possible explanation for the weak effect was the relatively small variation in these measures (coefficients of variation < 15%) across surveys because of the use of standardized protocols. The lack of a consistent relation between effort and detection over a time span with relatively large fluctuations in population sizes does bring into question the practice of expanding catch data using measures of effort. If there is no relation between catch and sampling effort or the underlying relationship is sharply non-linear, adjusting catch data by dividing raw counts by measures of effort (e.g., volume) could potentially introduce a false pattern in the data (Peterson and Paukert 2009). For example, assuming that the true relationship between catch and effort was asymptotic, dividing catch by effort would systematically underestimate abundance for instances where effort was greater. To avoid these potential biases, the relationship between catch and effort should be evaluated across a range of true abundances to establish whether linear assumptions are justifiable.

Interestingly, there was little evidence that tows at a station affected species detection in subsequent replicate tows. The probability of detecting the abundant state became lower after the first tow for Longfin Smelt in the 20-mm Survey and was the only evidence of a behavioral response of fish to replicate tows. This suggests that surveys that employ replicate tows are appropriate for accounting for incomplete detection or capture of fishes in the estuary. Species occupancy and the presence of the abundant state were strongly and consistently related to salinity and specific conductance, which is similar to previous analyses of long-term monitoring data collected in the estuary (Sommer and Mejia. 2013; Latour 2015; Mahardja et al. 2017).

The random effect median odds ratios were similar in magnitude to–or greater than–the salinity and specific conductance odds ratios, which suggested that a substantial portion of the variation in occupancy and abundance were not accounted for by the covariates. Our accounting for spatial and temporal dependence in our models for the 20-mm Survey is likely responsible for the differences between our estimates and those reported in a similar analysis of the 20-mm Survey catch data (Mahardja et al. 2017). The latter reported models that contained more covariates than this study and included multiple quadratic terms, but the authors did not account for violations of independence assumptions. Importantly, failure to account for dependence leads to biased low standard errors and measures of model fit and can result in a model with more parameters than can be supported by the data (Royle and Dorazio 2008). The large spatial effect means that some locations are persistently more occupied than others. The strong spatial and temporal structuring of fish distribution and abundance we observed in this study suggests that researchers account for these factors when analyzing data from these and other long-term surveys.

The station random effects represented the (static) predictable variation in occupancy or abundance from station to station. These spatial effects were unrelated to salinity, temperature, turbidity and the other covariates evaluated and included in the occupancy models. That is, these effects are above and beyond the effects of the covariates included in the analysis. For instance, assume that there is a collection of stations with identical values of covariates (e.g., salinity, temperature) and two are chosen at random. The median odds ratio is interpreted as ratio of the probabilities that two randomly chosen stations (or years) are occupied. They may represent some unknown or heretofore, unconsidered factor(s) that affect the abundance and distribution of the each species or could represent terms not considered in this analysis (e.g. three way interactions, high-order quadratic effects). These effects could be the result of factors such as spatial context and juxtaposition (e.g., distance from certain key features, habitat adjacent to a station) and unmeasured covariates that did not change across years. Failure to identify and incorporate these spatial effects could lead to improper inferences and poor management decision making. For instance, habitat suitability criteria that were developed using these or similar monitoring data that did not estimate and incorporate the influence of unknown spatial factors, but instead focused on many of the factors considered in this analysis (e.g., salinity, turbidity; Bever at al. 2016), are likely missing important (unknown) factors affecting the abundance and distribution of fishes in the estuary. The magnitude of these random effects suggests that identifying and understanding these unknown factors may assist in the management of these focal taxa.

The station by year interaction random effect suggested that the distribution and abundance of the four species in the estuary among stations varied from year to year. Further analyses of the random effects suggested significant shifts in fish distribution over the last two decades. Presumably, some of these shifts were a response to the record drought from 2012–2016, which is consistent with the observed trends in increased salinity and specific conductance over time. However, these systematic changes in occupancy through time at a station were unrelated, or were in addition, to the changes in the factors that were included in the occupancy analysis (e.g., salinity, temperature). Some of the shifts may be related to large-scale events that changed habitat characteristics of areas near monitoring stations, such as the flooding at Liberty Island in the northwest corner of the Delta. The distribution of animals can be influenced by population abundance and the distribution of resources (Fretwell 1972). Thus, the

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distributional shift may have been due in part to the systematic decreases in occupancy and abundance of each species over time. Such changes are likely inevitable over the course of a long-term monitoring program. Using these long-term monitoring data to infer patterns in fish distribution and abundance across the entire estuary requires the fundamental assumption that the monitoring stations are representative of all the conditions across the system. Many of these long-term stations, however, were not randomly selected and only include areas within the channel that can be safely sampled (Barnard et al. 2013; Sommer and Mejia 2013). Additionally, the large spatial effect represented by the station random effect indicated that there are unknown station characteristics that are unrelated to the variables in the best fitting models but significantly affect fish distribution and abundance. Therefore, assumptions regarding the representativeness of the long-term stations are tenuous. These patterns stress the importance of implementing a proper statistically based sample design that includes randomization and equally as important, a sample protocol and estimator that can account for imperfect detection; the initiation of the Enhanced Delta Smelt Monitoring Program (Newman et al. 2017) is a good start. We encourage managers to consider modifications to existing long-term protocols that includes the incorporation of new (randomly selected) stations and methods to increase their inference space and data quality.

CONCLUSIONS

The multistate occupancy models used in this study were employed primarily to evaluate the effects of incomplete capture on perceived changes in fish distribution and abundance. Dynamic occupancy models have been used to inform natural resource management decision-support models for a variety of systems that range from Golden Eagle conservation (Martin et al. 2011) to water resource management (Tyre et al. 2011; Freeman et al. 2013; Shea et al. 2015). These dynamic models incorporate the effect of management actions on meta-demographic rates to predict changes in occupancy states of focal taxa. The advantage of these approaches are that they allow for the seamless integration of monitoring data and management decision-support models; thereby facilitating adaptive management. For instance, Freeman et al. (2013) and Martin et al. (2009) incorporated alternative hypotheses of system dynamics affecting the occupancy of focal taxa and identified those that had the greatest influence on management decision making. These authors then implemented monitoring using multistate occupancy as a response and evaluated the evidence for their respective hypotheses on an annual basis (Martin et al. 2011; Peterson and Freeman 2016). The challenges faced by these studies and others that employed occupancy-based approaches to facilitate adaptive management were not unlike the challenges faced by managers in the estuary (e.g., broad spatial extents, limited budgets). Such an approach, however, will require the development of dynamic occupancy models that relate the influence of management actions and other external drivers on the meta-demographic rates of fishes in the estuary. The long-term monitoring data used in this study may prove useful in such an endeavor, but the interpretation and use of the resulting models will be limited to the inferential space of the data.

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