

Understanding imperfect detection in a San Francisco Estuary long-term larval and juvenile fish monitoring programme

B. Mahardja¹ | M. J. Young² | B. Schreier¹ | T. Sommer¹

¹Division of Environmental Services, California Department of Water Resources, West Sacramento, CA, USA

²Department of Wildlife, Fish & Conservation Biology, University of California – Davis, Davis, CA, USA

Correspondence

Brian Mahardja, Division of Environmental Services, California Department of Water Resources, Industrial Boulevard, West Sacramento, CA, USA.
Email: brian.mahardja@water.ca.gov

Present address

Brian Mahardja, Division of Environmental Services, California Department of Water Resources, Industrial Boulevard, West Sacramento, CA, USA.
Email: brian.mahardja@water.ca.gov

Abstract

Imperfect detection can present a significant challenge when monitoring for a rare and imperilled species. Here, a long-term larval and early-juvenile fish monitoring programme in the upper San Francisco Estuary was examined to evaluate its overall reliability in detecting various fish species, including the imperilled delta smelt, *Hypomesus transpacificus* McAllister, for which the programme was designed. Using occupancy modelling, detection probability of species with pelagic larval or juvenile life stages was found to be generally high (≥ 0.95) based on the current sampling effort of three larval net tows per site. However, detection probability can vary considerably from year to year depending on the species' level of larval production. Water temperature and turbidity were identified as important predictors of occurrence for young-of-year delta smelt, longfin smelt *Spirinchus thaleichthys* (Ayres) and striped bass *Morone saxatilis* (Walbaum), and there was evidence for fish size selectivity by the sampling gear in all three species. These results highlight the need to consider adaptively managing detection probability by increasing sampling effort in years when young-of-year delta smelt abundance is expected to be low, especially when information on the species' occurrence at a particular region is critical.

KEYWORDS

detection probability, early life history, estuarine ecology, *Hypomesus transpacificus*, *Morone saxatilis*, *Spirinchus thaleichthys*

1 | INTRODUCTION

Ecological monitoring programmes are developed to study the distribution or abundance of one or more species of interest. However, imperfect detection occurs in any sampling scheme, where a non-observation may be a result of either a true absence or a failure of detection (MacKenzie et al., 2002; Royle & Nichols, 2003). This problem is magnified when targeting rare or cryptic species whose information is often particularly crucial to researchers and managers (MacKenzie, Royle, Brown & Nichols, 2004). One such species is the delta smelt, *Hypomesus transpacificus* McAllister, a small-bodied, pelagic, annual fish endemic to the San Francisco Estuary (SFE), California.

The SFE has undergone dramatic morphological, hydrological, chemical and biological alterations since the onset of the California gold rush in the mid-1800s (Conomos, 1979; Lund et al., 2008). While the modern SFE continues to be a dynamic and complex ecosystem that supports important ecosystem services, numerous stressors have caused declines in multiple fish species (Bennett & Moyle, 1996; IEP MAST 2015; Sommer et al., 2007; Thomson et al., 2010). Once common in the freshwater and brackish portions of the SFE, the delta smelt population declined during the 1980s resulting in the species' listing as threatened under both the California and United States Endangered Species Acts in 1993 (USFWS 1993). Long-term declines in delta smelt and other pelagic SFE fishes culminated in a multispecies collapse in

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the early 2000s, dubbed the pelagic organism decline (Sommer et al., 2007; Thomson et al., 2010). Delta smelt have since been reclassified as endangered under California state law in 2009.

Recruitment is one of the primary drivers of fish population dynamics (Houde, 1987; Ricker, 1975), and it is particularly crucial for an annual species such as delta smelt whose population resiliency is dependent on sufficient recruitment each year (Bennett, 2005; IEP MAST 2015). To determine the vulnerability of larval and early-juvenile (i.e. young-of-year) delta smelt to entrainment at water export facilities in the upper SFE (Damon, 2015; Grimaldo et al., 2009), the California Department of Fish and Wildlife (CDFW) initiated an annual young-of-year fish monitoring programme in 1995, named the 20-mm Survey (based on the minimum size of delta smelt that can be considered as "entrained" in the water export facilities under the Endangered Species Act). Since 1995, data from the 20-mm Survey have been used to evaluate timing, distribution and reproductive success (i.e. young-of-year abundance) of the species (Dege & Brown, 2004; Kimmerer, Gross & MacWilliams, 2009; Kimmerer, MacWilliams & Gross, 2013; Sommer & Mejia, 2013). However, to date, there has been no published evaluation on the survey's sampling efficiency for its target species, the delta smelt.

The potential for imperfect detection is not accounted for in the reporting of the 20-mm Survey young-of-year delta smelt data (Damon, 2015; La Luz & Baxter, 2015). This may lead to errors in the estimates of young-of-year delta smelt distribution and relative abundance, particularly in low-abundance years. These errors could then propagate through analyses of population dynamics leading to spurious conclusions. In recent years, statistical methods have been developed to estimate the probability of detecting species at occupied sites based on multiple site visits (MacKenzie et al., 2002, 2006). This approach has provided valuable information for fisheries management, including describing species distribution for rare species (Albanese, Litts, Camp & Weiler, 2014; Albanese, Peterson, Freeman & Weiler, 2007), assessing habitat preferences (Falke, Fausch, Bestgen & Bailey, 2010), evaluating sampling protocols (Peoples & Frimpong, 2011; Williams & Fabrizio, 2011) and improving the precision of abundance indices (Pritt, DuFour, Mayer, Roseman & DeBruyne, 2014). Although site occupancy models have been applied to the sampling of larval or juvenile fishes (Falke et al., 2010; Pritt et al., 2014), none have used a long-term monitoring data set that spans decades and is comprises over 20,000 individual sampling events. This long-term data set is particularly valuable in that it allows researchers to assess empirically the relationship between annual relative abundance (in the form of fish count per volume) and detection probability.

Although specifically designed to monitor the delta smelt, the 20-mm Survey also captures a diversity of other young-of-year fishes (Dege & Brown, 2004), allowing for comparison of detection probabilities among species. In addition to the delta smelt, the 20-mm Survey captures several pelagic fish species of conservation or recreational interest such as longfin smelt, *Spirinchus thaleichthys* (Ayres) and striped bass *Morone saxatilis* (Walbaum), both of which also have declined substantially in the past decade (Mac Nally et al., 2010; Sommer et al., 2007; Thomson et al., 2010). Furthermore, the survey also provides data on highly abundant, yet understudied invasive fishes such as the Shimofuri goby, *Tridentiger bifasciatus* Steindacher, and Shokihaze

goby, *Tridentiger barbatus* (Günther; Moyle, 2002; O'rear & Moyle, 2010).

Given recent declines of multiple fish species in the SFE (Sommer et al., 2007; Thomson et al., 2010), an evaluation of the accuracy and reliability of the existing surveys are appropriate. The primary objective of this study was to understand how the efficiency (i.e. detection probability) of the 20-mm Survey sampling method varies across species and over time and how this variability in gear efficiency can potentially influence the survey's species distribution estimates. To examine how imperfect detection affects the accuracy of this long-term monitoring programme, this study addressed the following topics: (1) how detection probability varies among fish species; (2) the relationship between interannual abundance and detection probability; and (3) the environmental factors (e.g. tidal stage, turbidity, water temperature) that affect fish occupancy and detectability.

2 | METHODS

2.1 | Study area

The SFE (Figure 1) is the largest estuary on the Pacific coast of the United States and is typified by a Mediterranean climate (high precipitation in winter–spring and dry weather in summer–fall). The upstream region of the SFE is located at the confluence between the Sacramento and San Joaquin Rivers and their tributary channels; this region is referred to as the Sacramento-San Joaquin Delta (Delta). Although once a contiguous marsh ecosystem that drained into San Francisco Bay, the current Delta exists as a meandering network of freshwater tidal channels around leveed islands with managed freshwater flows (Kimmerer, 2004; Nichols, Cloern, Luoma & Peterson, 1986; Whipple, Grossinger, Rankin, Stanford & Askevold, 2012). Downstream of the Delta, fresh water flows west to Suisun Bay, Carquinez Strait and San Pablo Bay before reaching San Francisco Bay and ultimately the Pacific Ocean. In this study, the upper SFE was defined as the region bounded by Carquinez Strait and the upstream tidal extent of the Delta.

2.2 | Data source

The 20-mm Survey was initiated in 1995 by CDFW and is ongoing today (Dege & Brown, 2004). Sampling is conducted using a 1,600- μm nylon mesh conical plankton net that is 5.1 m long with a 1.5 m² mouth opening. An attached flow meter is used to estimate the volume of water sampled at each tow. Each sample consists of three replicate 10-min stepped oblique tows, with 1.2 m of line reeled in per step to effectively sample the entire water column. At the end of each tow, fish are collected in a removable 2.2-L cod-end jar screened with 474- μm stainless steel mesh and transferred into jars containing 10% formalin neutralised with sodium borate. Rose bengal dye is added to each holding jar to help distinguish fish from detritus. Preserved fish are identified to species or lowest possible taxon and counted in the laboratory. The first 50 fish from each tow are randomly selected for fork length (*FL*, mm) except for delta smelt, which are always measured regardless of counts. Water temperature, conductivity and Secchi depth (cm) are measured with each sample.

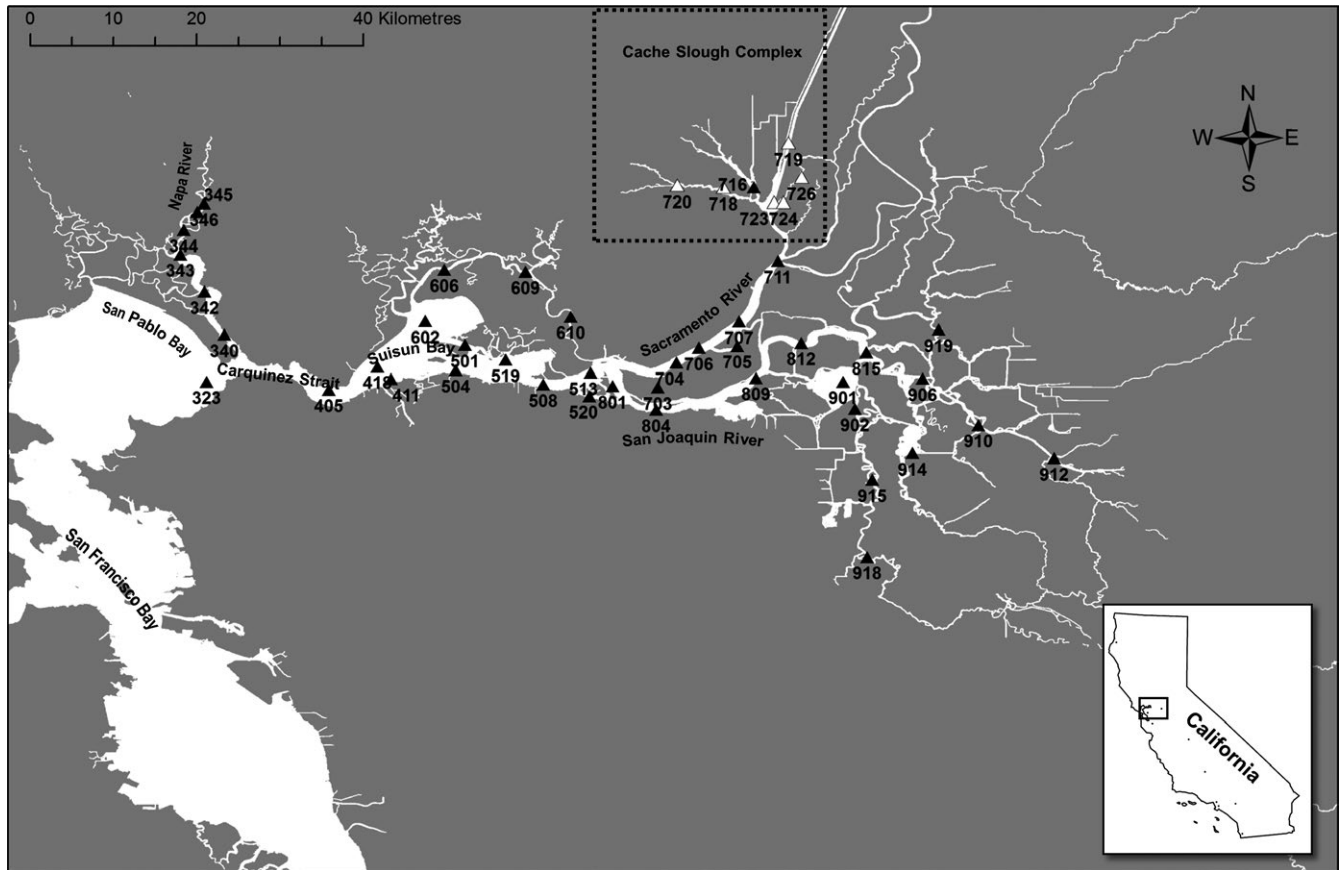


FIGURE 1 Sampling stations in the San Francisco Estuary used in California Department of Fish and Wildlife 20-mm Survey. Black triangles are 41 index stations that have been continuously sampled since 1995; white triangles in the Cache Slough Complex were added as part of regular monitoring in 2008

Data collected from the time period between 1995 and 2015 were used for this analysis. Each “survey” consisted of sampling conducted at every station over the period of one week. Surveys started each year in March or April and continued roughly every two weeks until mid- to late summer (July–August). Each survey was assigned numbers by the order in which they were done within a given year (e.g. survey one of 1995, survey two of 1995) and continued until a total of eight or nine surveys was reached for the year. The 20-mm Survey regularly sampled 41 stations between 1995 and 2007, and 47 stations starting in 2008 when six sites within the Cache Slough complex were added to the monitoring programme (Figure 1). Sampled sites included a variety of estuarine habitats (e.g. river channels, backwater sloughs, shallow bays and flooded islands) selected to encompass the spring and summer range of young-of-year delta smelt. Each site was targeted for sampling every survey, although certain sites were occasionally excluded for various reasons (see Table S1 for details).

2.3 | Data analysis

2.3.1 | Objective 1: Assessment of detection probability variation among fish species

The 10 taxa with the highest total catch count throughout the study period (1995–2015) were selected for analysis (Table 1). Of the 10

taxa, six are associated with pelagic habitat throughout their life history and four have pelagic larval-juvenile life stages with demersal adult form. Due to the difficulty and inconsistencies associated with the identification of Shimofuri and Shokihaze gobies, the total catch of the two species were combined into *Tridentiger* spp. Because the top 10 taxa exhibit a pelagic life history as larvae and juveniles, the three most commonly caught fish species associated with littoral habitat for all life stages [three-spine stickleback, *Gasterosteus aculeatus* L., Mississippi silverside, *Menidia audens* Hay, and Sacramento splittail *Pogonichthys macrolepidotus* (Ayres)] were added into the analysis for comparison purposes. Using size cut-offs from the literature (Moyle, 2002), adult fish caught in the 20-mm Survey were removed from the data set to allow for a more accurate analysis of young-of-year fish detection probabilities (Fig. S1).

To estimate detection probability for each species, the MacKenzie et al. (2002) single-season, single-species occupancy model was used via the “unmarked” package (Fiske & Chandler, 2011) in R (R Development Core Team 2015). As part of this analysis, fish count data were converted to occurrence data, where “1” denoted presence and “0” denoted absence of the species within a tow. In the MacKenzie et al. (2002) species occupancy model, the probability of observing a certain detection history is considered a product of the probability that the site is occupied by the species (ψ) and the probability of detecting



TABLE 1 Top 19 species categories ordered by total catch numbers for the 20-mm Survey between 1995 and 2015

| Common name | Scientific name | Total number of individuals caught | Dominant habitat type |
|--|---|------------------------------------|--------------------------|
| <i>Tridentiger</i> spp.^a | <i>Tridentiger</i> spp.^a | 580,207 ^a | Demersal; pelagic larvae |
| Longfin smelt | <i>Spirinchus thaleichthys</i> (Ayres) | 539,322 | Pelagic |
| Pacific herring | <i>Clupea pallasii</i> Valenciennes | 226,892 | Pelagic |
| Striped bass | <i>Morone saxatilis</i> (Walbaum) | 223,004 | Pelagic |
| Threadfin shad | <i>Acanthogobius flavimanus</i> (Günther) | 150,939 | Pelagic |
| Yellowfin goby | <i>Dorosoma petenense</i> (Temminck & Schlegel) | 150,243 | Demersal; pelagic larvae |
| Delta smelt | <i>Hypomesus transpacificus</i> McAllister | 26,823 | Pelagic |
| Northern anchovy | <i>Engraulis mordax</i> Girard | 22,856 | Pelagic |
| Prickly sculpin | <i>Cottus asper</i> Richardson | 17,880 | Demersal; pelagic larvae |
| Shimofuri goby^a | <i>Tridentiger bifasciatus</i>^a Steindacher | 15,898 ^a | Demersal; pelagic larvae |
| White catfish | <i>Ameiurus catus</i> (L.) | 11,634 | Demersal |
| Bay goby | <i>Lepidogobius lepidus</i> (Girard) | 10,350 | – |
| American shad | <i>Alosa sapidissima</i> (Wilson) | 6,237 | Pelagic |
| Channel catfish | <i>Ictalurus punctatus</i> (Rafinesque) | 5,868 | Demersal |
| Three-spine stickleback | <i>Gasterosteus aculeatus</i> L. | 5,120 | Littoral |
| Arrow goby | <i>Clevelandia ios</i> (Jordan & Gilbert) | 3,685 | Demersal |
| Mississippi silverside | <i>Menidia audens</i> Hay | 2,285 | Littoral |
| Cheekspot goby | <i>Ilypnus gilberti</i> (Eigenmann & Eigenmann) | 1,791 | – |
| Sacramento splittail | <i>Pogonichthys macrolepidotus</i> (Ayres) | 1,553 | Littoral |

Taxa labeled in bold were analysed in this study. Dominant habitat type classification is based on information in Moyle (2002).

^aShimofuri goby, shokihaze goby [*Tridentiger barbatus* (Günther); not shown], and data from the unidentified *Tridentiger* spp. category were grouped together into the *Tridentiger* spp. category and were analysed as a single group due to high possibility of misidentification between the two species.

the species given that it is present at the site (p). For example, if p is constant between tows, a sample with the detection history of 0, 0 and 1 (undetected in tow 1, undetected at tow 2, detected at tow 3) can be expressed as:

$$\Pr(001) = \varphi(1-p)(1-p)(p),$$

However, in the case where the sample contains all non-detections, this may be due to the species being absent at the site or that the site was occupied but the species was undetected. Therefore, the probability of detection history for three consecutive zeroes (0, 0, 0) can be expressed as:

$$\Pr(000) = \varphi(1-p)(1-p)(1-p) + (1-\varphi).$$

Once the probability statements for all samples are constructed, the occupancy and detection probability parameters (ψ and p , respectively) are estimated by maximum likelihood (MacKenzie et al., 2002). In this model, parameters are also allowed to be a function of covariates to account for heterogeneity in occupancy or detection probabilities. For instance, occupancy probability can be constructed as a function of one or more environmental variables (e.g. water temperature, turbidity). Covariates are entered into the model by way of the logistic regression model with a logit-link function.



To allow for an easily interpretable comparison of detection probabilities among species, identical occupancy models were used for each of the 12 species (Table 1). For each species, the occupancy model was constructed with year as a categorical variable for occupancy probability and a constant detection probability (i.e. no covariate). The model fitted was $\Psi(\text{year})p(\cdot)$, where “.” denotes a constant. Year (1995–2015) was included as a categorical variable for occupancy to reduce bias introduced from years of extreme high or low abundance or exceedingly narrow or wide distribution. The year 1995 was used as the reference categorical variable for the model. The probability of detecting the species at least once, given a sampling effort (number of tows; N) and their presence at the site, was then calculated using: $1 - (1 - p)^N$.

2.3.2 | Objective 2: Assessment of the relationship between interannual abundance and detection probability

One of the more significant sources of variation in detection probability is a species' overall abundance (Royle & Nichols, 2003). To evaluate the linkage between abundance and detection probabilities, annual density indices for select species were compared with their estimated annual detection probabilities. Three species (delta smelt, longfin smelt and striped bass) were chosen for this analysis based on the high overlap between the 20-mm Survey sampling effort and their young-of-year timing and distribution. To assess interannual variation in detection probability, a site occupancy model was constructed for each species that assigned year (1995–2015) as categorical variable for both occupancy and detection probabilities: $\Psi(\text{year})p(\text{year})$. This model was compared to the model used in Objective 1 to determine if the heterogeneous detection probability model was a better fit, thus providing evidence for interannual variation in detection probability. Akaike's information criterion adjusted for sample size (AICc) was used for model comparisons (Hurvich & Tsai, 1991). Annual detection probabilities were then calculated by adding each year's coefficient (1996–2015) to the reference year's (1995) coefficient and inverse logit transforming the resulting values.

To compare species' relative abundance between years, an annual density index for each species was calculated by modifying CDFW's 20-mm Survey delta smelt index (Damon, 2015; La Luz & Baxter, 2015; IEP MAST 2015). Water volume sampled per tow (m^3) was first calculated by multiplying the area of the net's mouth opening (1.5 m^2) by the following:

$$(\text{Flow Meter}_{\text{Finish}} - \text{Flow Meter}_{\text{Start}}) * 0.27,$$

where 0.27 is the calibration factor. Number of fish per $10,000 \text{ m}^3$ was then calculated for each tow and averaged for each sample (up to three tows per sample). Mean catch per $10,000 \text{ m}^3$ for each survey week was then calculated for the three species and the values were subsequently $\log_{10}(1 + X)$ -transformed, where X is catch per $10,000 \text{ m}^3$, to reduce excessive spread in values resulting from the pelagic fish community collapse in the mid-2000s (Mac Nally et al., 2010; Sommer et al., 2007; Thomson et al., 2010).

The final annual density indices for the three species were calculated by averaging these $\log_{10}(1 + X)$ -transformed values over a specific subset of surveys for each year. A set of four surveys each year were used for calculating the delta smelt annual density index: two surveys before and two surveys after young-of-year delta smelt reach an average FL of 20 mm (Damon, 2015; La Luz & Baxter, 2015). A set of three surveys each year in which young-of-year longfin smelt averaged about 20 mm in FL were chosen for calculating the longfin smelt annual density index. For striped bass, a set of three surveys each year in which young-of-year striped bass averaged roughly 15 mm FL were chosen. The inexact criteria for longfin smelt and striped bass were chosen because there were years when these non-target species either never reached the target average FL by the last survey of the year or already exceeded the target average FL in the first survey of the year. The subset of surveys selected for the annual density index generally occurred during mid-May to early June for delta smelt, late April to mid-May for longfin smelt and mid- to late June for striped bass (see Table S2).

Given that detection probability ranges between 0 and 1, logistic regression was used to evaluate the correlation between the resulting annual density indices and annual detection probabilities. All three species were combined in this analysis to evaluate if and how species differ in their abundance–detectability relationships. A model ranking procedure using AICc was then conducted for following global model and its nested models:

$$p = \beta_0 + \beta_1 \text{Index} + \beta_2 \text{Species} + \beta_3 \text{Index} \times \text{Species},$$

where p is the species detection probability at a given year. When applicable, delta smelt was used as the reference species.

2.3.3 | Objective 3: Identification of environmental factors that affect fish occupancy and detectability

To identify the environmental factors that predict the detection probability and occupancy for delta smelt, longfin smelt and striped bass, a model selection analysis was conducted separately for each species with a suite of possible occupancy and detection covariates. Covariates tested for occupancy probability included the categorical variable of tidal stage (high, ebb, low and flood) and the continuous variables of day of year, Secchi depth, conductivity and relative temperature. Day-of-year variable was included to adjust for the spawning date of each species, and a tidal stage variable was included based on previous evidence that delta smelt can occupy different areas based on the tide (Bennett & Burau, 2015). The quadratic terms for Secchi depth and conductivity were also included as covariates because their relationship to fish occupancy may be nonlinear. Relative temperature was used instead of the recorded temperature ($^{\circ}\text{C}$) due to the inherent collinearity between day of year and temperature. Relative temperature was measured by first constructing an ordinary least squares (OLS) linear regression between day of year and temperature using the 21-year data set from the 20-mm Survey (1995–2015) with temperature as the response variable ($r^2 = .66, p < .001$). Relative



temperature values were then acquired by calculating the residual of each observation (subtracting the sample's recorded temperature from the predicted daily temperature of the model). Year was fixed as a categorical variable for the occupancy portion of all models tested because occupancy for larval and juvenile fish will inevitably vary year to year. Collinearity between occupancy covariates was assessed by ensuring that all covariate pairs had $|r| < .7$ (Dormann et al., 2013). The full model contained the following occupancy submodel:

$$\Psi(\text{Year} + \text{Tide} + \text{Temperature} + \text{Day of year} + \text{Secchi depth} + \text{Secchi depth}^2 + \text{Conductivity} + \text{Conductivity}^2).$$

For detection probability, the following covariates were considered: year (categorical), tidal stage (categorical), predicted fish length (continuous) and the quadratic term for predicted fish length. The full model contained the following detection submodel:

$$p(\text{Year} + \text{Tide} + \text{Predicted Length} + \text{Predicted Length}^2)$$

Due to imperfect detection, false absence (type-II error) can occur in a sample where fish are actually present at a location but no fish were captured or measured. For this reason, predicted fish length was used instead of actual recorded fork length (mm) as a proxy for the species' overall mean length at the time of sampling. Predicted length was acquired using an OLS regression on fish fork length based on date and year, using the available length data for each species. For each species, the OLS length prediction model consisted of day of year, year as categorical variable and the interaction term between the day of year and year. The full OLS length prediction models with interaction terms were used for all three species because they all have lower AICc relative to the nested models.

Prior to the model selection analysis, all continuous variables (for both occupancy and detection) were z-score-transformed. Models were compared using all possible combinations of occupancy and detection covariates, aside from the fixed year covariate for occupancy and the removal of models that contain a quadratic term without its corresponding linear term. When applicable, reference categorical variables were 1995 for year and high tide for tidal stage. Note that because each location is sampled for different numbers of times depending on the year (see Table S1), occupancy results from this analysis are generally, but not exactly, proportional to sites occupied.

Model fit for the single-season occupancy model was assessed by calculating the overdispersion parameter \hat{c} for each species' global model (MacKenzie & Bailey, 2004) using the "AICcmodavg" package (Mazerolle, 2016). Due to the size of the data set (>7,000 samples for three species), calculation of \hat{c} was made with just 1,000 bootstraps to avoid exceedingly long calculation time. The goodness-of-fit tests suggested overdispersion for all three species and that the single-season occupancy models may be underfitting the data ($\hat{c} > 4$). This appeared to be caused by a larger than expected number of samples where fish are caught in all three tows and a lower than expected number of samples where fish are caught twice in a row (suggesting some depletion effect or trap response). To adjust for the poor fit and further evaluate

the single-season occupancy model selection results, a spatial dependence occupancy model (Hines et al., 2010) was run for all three species using the program PRESENCE version 12.0 (Hines, 2006) and the same combination of covariates. A forward stepwise model selection approach by AICc (starting with the detection probability submodel) was used to select the best spatial dependence occupancy model for each species.

Once the best single-season and spatial dependence models were identified, model-averaged predictions (Burnham & Anderson, 2002) using the full raw data set as input were created to evaluate general trends over the study period of proportion of sites occupied by each species. Only models with an Akaike weight >0.01 (shown in Tables 3 and 4) were considered for model-averaging purposes. Two-sided Mann-Kendall's tau tests (Mann, 1945) on the median annual estimates were then used to assess whether or not there was a statistically significant change ($\alpha = .05$) in overall occupancy of the three species over the study period (1995–2015).

3 | RESULTS

3.1 | Objective 1: Assessment of detection probability variation among fish species

The overall probability of detection for larval or juvenile fishes by the 20-mm Survey varied among taxa and life histories (Figure 2). Among the fully pelagic species [delta smelt, longfin smelt, northern anchovy, *Engraulis mordax* Girard, Pacific herring, *Clupea pallasii* Valenciennes, striped bass and threadfin shad, *Dorosoma petenense* (Günther)], overall detection probability was generally high, estimated to be ≥ 0.95 after three tows. Within this group, striped bass had the greatest detection probability (0.83 for one tow) and delta smelt had the lowest detection probability (0.63 for one tow). High detection probabilities were also observed among the three demersal taxa with pelagic larvae that were analysed: prickly sculpin, *Cottus asper* Richardson, *Tridentiger* spp. and yellowfin goby, *Acanthogobius flavimanus* (Temminck & Schlegel). Cumulative detection probability was ≥ 0.95 after three tows for all three species. Results from the *Tridentiger* species group likely reflect the biology of the much more abundant Shimofuri goby (Dege & Brown, 2004; Greiner, 2002). In contrast, the primarily littoral species (three-spine stickleback, Sacramento splittail and Mississippi silverside) all shared relatively low detection probabilities. Based on the analysis, at least four to five replicate tows by the 20-mm Survey were needed to reach >0.95 cumulative detection probability at a site for these three littoral species.

3.2 | Objective 2: Assessment of the relationship between interannual abundance and detection probability

Delta smelt, longfin smelt and striped bass all showed evidence of interannual variation in detection probability, as models with variable detection probability by year had lower AICc scores than

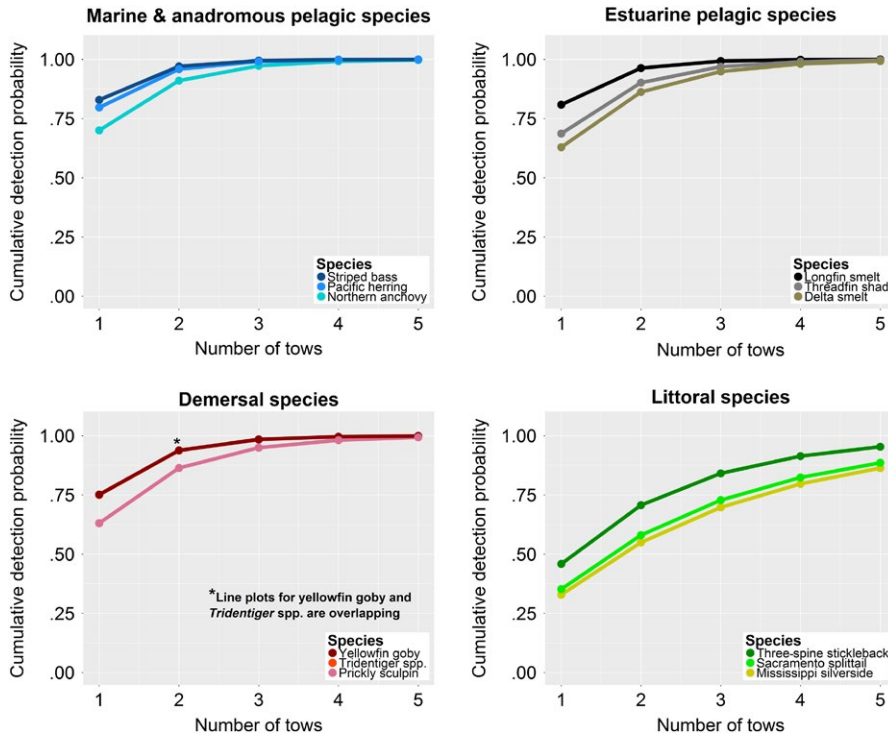


FIGURE 2 Cumulative detection probability (probability of at least one detection given that taxon is present) by taxon, habitat association and number of tows. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Regression coefficients and AICc for the logistic regression models used to examine the relationship between young-of-year fish densities and detection probability (response variable was the estimated annual detection probabilities for the three species)

| Model | Intercept | Annual density index | Species categorical term | | Interaction term | | AICc |
|-------|-----------|----------------------|--------------------------|--------------|---------------------|--------------------|-------|
| | | | Longfin smelt | Striped bass | Longfin smelt:index | Striped bass:index | |
| 1 | -0.7298 | 0.5436* | - | - | - | - | 44.73 |
| 2 | 1.0101* | - | - | - | - | - | 49.28 |
| 3 | -0.5749 | 0.4217 | 0.2370 | 0.5366 | - | - | 49.40 |
| 4 | -0.9842 | 0.6136 | 0.9682 | 1.6114 | -0.2752 | -0.3686 | 53.14 |

Reference species for categorical variable and interaction term is delta smelt.

*Significance at $p < .05$.

models without (Table 2). Annual density index and detection probability estimates were generally lower for delta smelt than for longfin smelt and striped bass (Figure 3). Within the study period (1995–2015), the annual density index for delta smelt ranged from 0.2 (2007) to 3.4 (2000) and their annual detection probability estimates ranged from 0.24 (2007) to 0.75 (1996). Annual density indices for longfin smelt and striped bass ranged from 2.0 (2015) to 5.5 (2000) and from 2.4 (2014) to 5.2 (1995), respectively. Annual detection probabilities for the two species ranged from 0.60 (2015) to 0.92 (2002) for longfin smelt and from 0.76 (2014) to 0.87 (2005) for striped bass. Of the logistic regression models testing the relationship between relative abundance and detection probabilities, the model that included only the annual density index covariate (i.e. no difference in slope and intercept between species) had the lowest AICc value (Table 2). The annual density index covariate in this best-fitting model was significant at $p < .05$ and its coefficient value was positive, demonstrating that a positive relationship exists between abundance and detection probability.

3.3 | Objective 3: Identifying environmental factors that affect fish occupancy and detectability

For delta smelt, the top seven single-season models ranked by AICc accounted for >99% of the Akaike weight out of the 864 single-season models tested (Table 3 and Table S3). Day of year, Secchi depth, conductivity and temperature were all represented in the occupancy portion of the top single-season models for delta smelt (Table 3 and Tables S3, S4). Predicted fish length, its quadratic term and year were also included in the detectability portion of all top single-season models. Four spatial dependence models represented >99% of the Akaike weight out of the spatial dependence models tested (Table 4 and Tables S5, S6). Conductivity, Secchi depth and temperature were occupancy covariates in all six best models. Similar to the single-season models, year, predicted fish length and its quadratic term were included in all of the top spatial dependence models. Detection probability by the 20-mm Survey for delta smelt was predicted to be optimal at ~25 mm FL by the single-season models and was estimated to

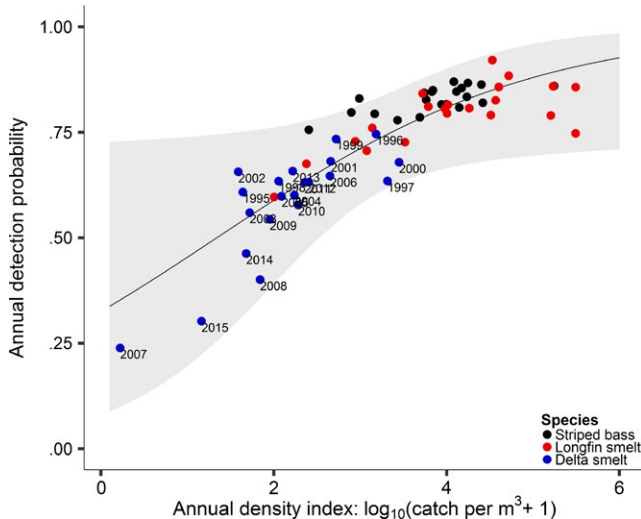


FIGURE 3 Logistic regression model depicting the relationship between annual density index of delta smelt, longfin smelt and striped bass with their respective detection probability. Best model by AICc (model 1) from Table 2 shown. Model prediction is shown by solid black line, and 95% confidence intervals are indicated by the grey shaded areas. Points are the observed values for all three species between 1995 and 2015. Years for delta smelt are shown. [Colour figure can be viewed at wileyonlinelibrary.com]

peak and asymptote at ~ 15 mm FL by the spatial dependence models (Figure 4). Model-averaged predictions of delta smelt occupancy were highly variable from year to year, but their annual median followed an overall declining trend over the study period for both types of occupancy model (Figure 5; two-sided Mann–Kendall's tau test, $p < .01$).

The top four longfin smelt single-season models accounted for $>99\%$ of the Akaike weight out of all the single-season models tested (Table 3 and Tables S3, S4). Every covariate, with the exception of tide, was represented in all four best single-season models. The detection probability portion of the top single-season models contained both linear and quadratic predicted length terms along with year. Three models represented $>99\%$ of the Akaike weight out of the spatial dependence models tested, all of which contained Secchi depth, temperature and day of year as covariates for occupancy and predicted length, its quadratic term, year and tide as covariates for detection probability (Table 4 and Tables S5, S6). Peak detection probability by the 20-mm Survey for longfin smelt was estimated to be at ~ 14 mm FL by the single-season models (Figure 4), and the spatial dependence models estimated detection probability to generally be near 100% until longfin smelt reaches a size of ~ 35 mm FL. Day-of-year coefficient for all longfin smelt occupancy models was negative, indicating that the 20-mm Survey generally occur after the spawning period of longfin smelt (Tables S3, S5). There was no clear temporal trend for the species' occupancy ($p > .05$) based on their annual median values for both the single-season and spatial dependence models (Figure 5).

Nine striped bass single-season models accounted for $>99\%$ of the Akaike weight out of the single-season models tested. In this group of nine single-season models, Secchi depth, day of year and conductivity were always represented in the occupancy portion while predicted

length, its quadratic term and year were all represented in the detection probability portion (Table 3 and Tables S3, S4). The two best ranked spatial dependence models accounted for essentially all of the Akaike weight out of the spatial dependence models tested. The top spatial dependence models had Secchi depth, conductivity, temperature and day of year in the occupancy portion of the models and predicted length, its quadratic term and year in the detection probability portion of the models (Table 4 and Tables S5, S6). Peak detection probability for striped bass was estimated to be at ~ 14 mm FL by the single-season models and the spatial dependence model estimated striped bass detectability to be high ($>99\%$) until the species reaches a size of ~ 18 mm FL (Figure 4). The day-of-year coefficient for all striped bass occupancy models was positive, indicating that the 20-mm Survey generally starts prior to the striped bass spawning period (Tables S3, S5). Model-averaged predictions for striped bass occupancy from both occupancy model types appeared to have declined over time based on annual median values (Figure 5; two-sided Mann–Kendall's tau test, $p < .01$).

4 | DISCUSSION

Overlooking imperfect detection in ecological monitoring can result in biased estimation of species abundance and distribution (MacKenzie et al., 2006). Prior to this study, SFE fisheries managers have had minimal quantitative information on the role of imperfect detection in their long-term monitoring programmes. Here, it was demonstrated that on average the SFE 20-mm Survey is fairly effective at monitoring species with pelagic juvenile or larval life stages with the existing sampling effort (three tows per site). However, these detection probabilities vary considerably from year to year depending on the species' annual young-of-year production. This variability is of particular importance for the endangered delta smelt, as their young-of-year abundance has reached such low levels in recent years that the three replicate net tows would result in a cumulative detection probability well below 0.95. These results highlight the need to consider the relationship between abundance and detection probability when monitoring species in precipitous decline.

4.1 | Interspecific variation of detection probability

One common contributor to variation in detection probabilities among species is life history "trait" (Pritt et al., 2014). Of the 12 species for which we estimated overall detection probability, nine were considered to be pelagic as larvae or juveniles, spending this part of their life stage in offshore habitats. For these species, overall cumulative detection probabilities (21 year average) were estimated to be $\geq 95\%$ after three repeated net tows. These general detection probability estimates were higher than expected, considering that this group includes the imperilled delta smelt. By contrast, the three fully littoral fish species that were analysed (three-spine stickleback, Mississippi silverside and Sacramento splittail) exhibited the three lowest detection probabilities. Three-spine stickleback had the highest detection probability in this group, with just 84% cumulative detection probability after



TABLE 3 Summary table of best single-season occupancy models by Akaike weight (w_i) for the three pelagic fish species chosen for model selection analysis

| Species | Model | AICc | Δ AICc | w_i | Cumulative w_i |
|---------------|--|----------|---------------|-------|------------------|
| Delta smelt | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14255.51 | 0.00 | 0.39 | 0.39 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{length} + \text{length}^2)$ | 14255.85 | 0.34 | 0.33 | 0.72 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{length} + \text{length}^2)$ | 14257.40 | 1.89 | 0.15 | 0.87 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14258.76 | 3.25 | 0.08 | 0.94 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond}), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14261.24 | 5.73 | 0.02 | 0.97 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond}), p(\text{year} + \text{length} + \text{length}^2)$ | 14261.46 | 5.96 | 0.02 | 0.99 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond}), p(\text{year} + \text{length} + \text{length}^2)$ | 14263.14 | 7.63 | 0.01 | 1.00 |
| Longfin smelt | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{length} + \text{length}^2)$ | 13553.48 | 0.00 | 0.46 | 0.46 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 13555.07 | 1.59 | 0.21 | 0.67 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{length} + \text{length}^2)$ | 13555.52 | 2.03 | 0.17 | 0.84 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 13555.62 | 2.14 | 0.16 | 1.00 |
| Striped bass | $\Psi(\text{year} + \text{tide} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14933.07 | 0.00 | 0.47 | 0.47 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14934.00 | 0.93 | 0.30 | 0.77 |
| | $\Psi(\text{year} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14937.45 | 4.37 | 0.05 | 0.82 |
| | $\Psi(\text{year} + \text{tide} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14937.69 | 4.61 | 0.05 | 0.87 |
| | $\Psi(\text{year} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14938.27 | 5.19 | 0.04 | 0.91 |
| | $\Psi(\text{year} + \text{tide} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14938.41 | 5.34 | 0.03 | 0.95 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond} + \text{cond}^2), p(\text{year} + \text{length} + \text{length}^2)$ | 14938.59 | 5.52 | 0.03 | 0.98 |
| | $\Psi(\text{year} + \text{tide} + \text{temp} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond}), p(\text{year} + \text{tide} + \text{length} + \text{length}^2)$ | 14939.66 | 6.58 | 0.01 | 0.99 |
| | $\Psi(\text{year} + \text{tide} + \text{day} + \text{secchi} + \text{secchi}^2 + \text{cond}), p(\text{year} + \text{length} + \text{length}^2)$ | 14942.87 | 9.80 | 0.01 | 1.00 |

Models ranked by w_i are shown until cumulative w_i approximates 1.

Ψ = probability of occupancy, p = detection probability, day = day of year, secchi = Secchi depth, cond = conductivity, temp = relative temperature and length = predicted length by date.

three tows. While the abundance trend of three-spine stickleback within the SFE is not well understood, Mississippi silverside is one of the most common species in the freshwater-mesohaline portion of the upper SFE (Bennett & Moyle, 1996; Mahardja, Conrad, Lusher & Schreier, 2016; Matern, Moyle & Pierce, 2002; Nobriga, Feyrer, Baxter & Chotkowski, 2005) and juvenile Sacramento splittail are abundant and widely distributed in wet years (Feyrer, Sommer & Baxter, 2005;

Mahardja et al., 2015; Moyle, Baxter, Sommer, Foin & Matern, 2004; Sommer, Baxter & Herbold, 1997). The low catches and detection probabilities for these three species suggest that their catch by the 20-mm Survey is largely incidental and the survey cannot be relied upon to reflect accurately their distribution or annual relative abundance. Results from the interspecific detection probability comparison suggest that the overall detection probability of the 20-mm Survey

TABLE 4 Summary table of best spatial dependence occupancy models by Akaike weight (w_i) for the three pelagic fish species chosen for model selection analysis

| Species | Model | AICc | Δ AICc | w_i | Cumulative w_i |
|---------------|---|----------|---------------|-------|------------------|
| Delta smelt | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13812.35 | 0.00 | 0.33 | 0.33 |
| | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day} + \text{tide}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13813.01 | 0.66 | 0.24 | 0.57 |
| | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{tide}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13813.09 | 0.74 | 0.23 | 0.80 |
| | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13813.53 | 1.18 | 0.19 | 0.99 |
| Longfin smelt | $\Psi(\text{year} + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2 + \text{tide})$ | 13214.97 | 0.00 | 0.46 | 0.46 |
| | $\Psi(\text{year} + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day} + \text{tide}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2 + \text{tide})$ | 13215.69 | 0.72 | 0.32 | 0.78 |
| | $\Psi(\text{year} + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day} + \text{cond}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2 + \text{tide})$ | 13216.43 | 1.46 | 0.22 | 1.00 |
| Striped bass | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day} + \text{tide}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13754.50 | 0.00 | 0.92 | 0.92 |
| | $\Psi(\text{year} + \text{cond} + \text{cond}^2 + \text{secchi} + \text{secchi}^2 + \text{temp} + \text{day}), \theta'(\cdot), \theta(\cdot), \pi(\cdot), p(\text{year} + \text{length} + \text{length}^2)$ | 13759.38 | 4.88 | 0.08 | 1.00 |

Models ranked by w_i are shown until cumulative w_i approximates 1. Ψ = probability of occupancy, θ' = probability of species presence in a tow given that it was present in the previous tow, θ = probability of species presence in a tow given that it was not present in the previous tow, π = probability of species presence in first tow given that species is present at location prior to tow, p = detection probability conditional on species being present at the given tow, day = day of year, secchi = Secchi depth, cond = conductivity, temp = relative temperature and length = predicted length by date.

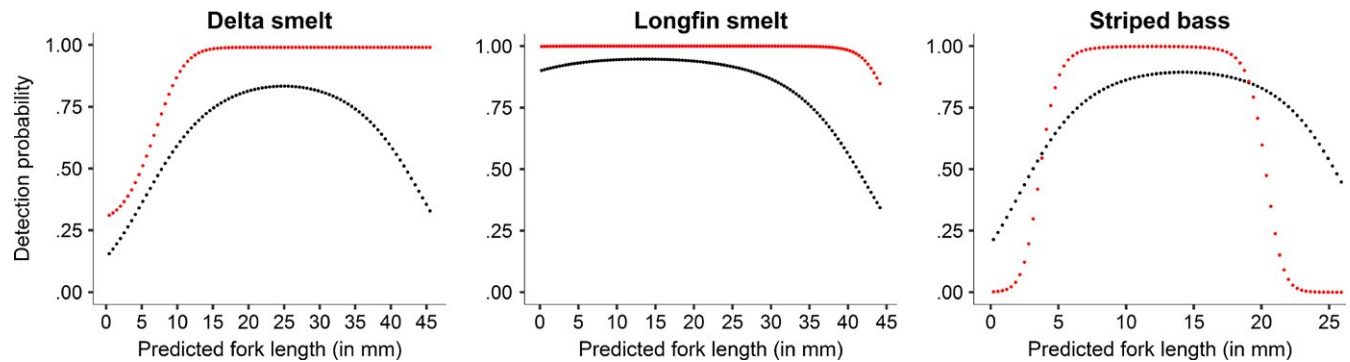


FIGURE 4 Predicted relationships between mean fish size and detectability by the survey method for delta smelt, longfin smelt and striped bass. Model-averaged predictions for the top-ranked single-season models are shown by the black dotted lines, and model-averaged predictions for the top-ranked spatial dependence models are shown by the red dotted lines. When applicable, the year 1996 and ebb tide were used as inputs. [Colour figure can be viewed at wileyonlinelibrary.com]

over the study period for the target species, the delta smelt, is fairly high. Moreover, given the similarly high detection probability estimates for other pelagic fish species by the 20-mm Survey, it seems that only slight adjustments would be needed for this monitoring programme to be able to monitor other pelagic fish species effectively.

4.2 | Interannual variation of detection probability

The general positive relationship between abundance and detectability suggests that while the 20-mm Survey has been fairly effective overall in the span of two decades, the rate of type-II error (i.e. a false negative) can be considerably high in years when species are low in

abundance. From a statistical standpoint, additional tows might be considered for the 20-mm Survey during years when delta smelt (or other species of interest) are expected to have low densities. It is feasible to conduct an approximate forecasting of delta smelt abundance in advance of the 20-mm Survey each year given that the life history and habitat of delta smelt has been well described in the literature (Moyle, Herbold, Stevens & Miller, 1992; Bennett, 2005; Sommer, Mejia, Nobriga, Feyrer & Grimaldo, 2011; Sommer & Mejia, 2013; IEP MAST 2015; Moyle, Brown, Durand & Hobbs, 2016) and various quantitative models for the species exist (Feyrer, Newman, Nobriga & Sommer, 2011; Feyrer, Nobriga & Sommer, 2007; Miller, Manly, Murphy, Fullerton & Ramey, 2012; Nobriga, Sommer, Feyrer & Fleming, 2008;

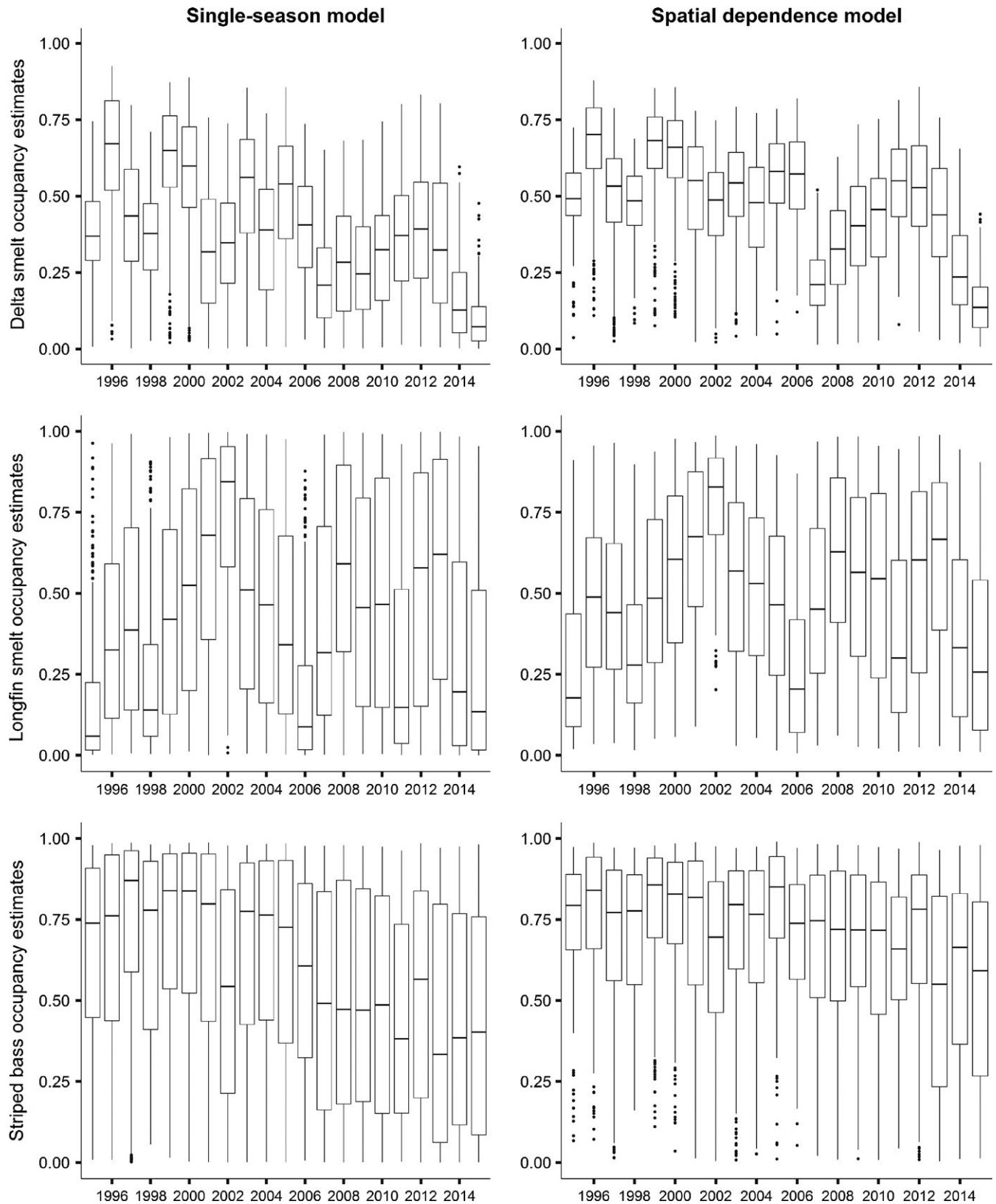


FIGURE 5 Model-averaged predictions of occupancy for the data set based on the top-ranked single-season models (left) and spatial dependence models (right). Predictions use raw data as input and are separated by year. Boxplots represent the interquartile range of predictions, line inside box is the median, and the whiskers represent the highest or lowest value that is within 1.5 of the interquartile range. Outliers are shown as points beyond the end of each whisker. The wide range of points reflects the wide range of occupancy and detection probabilities across the spatiotemporal extent of the survey

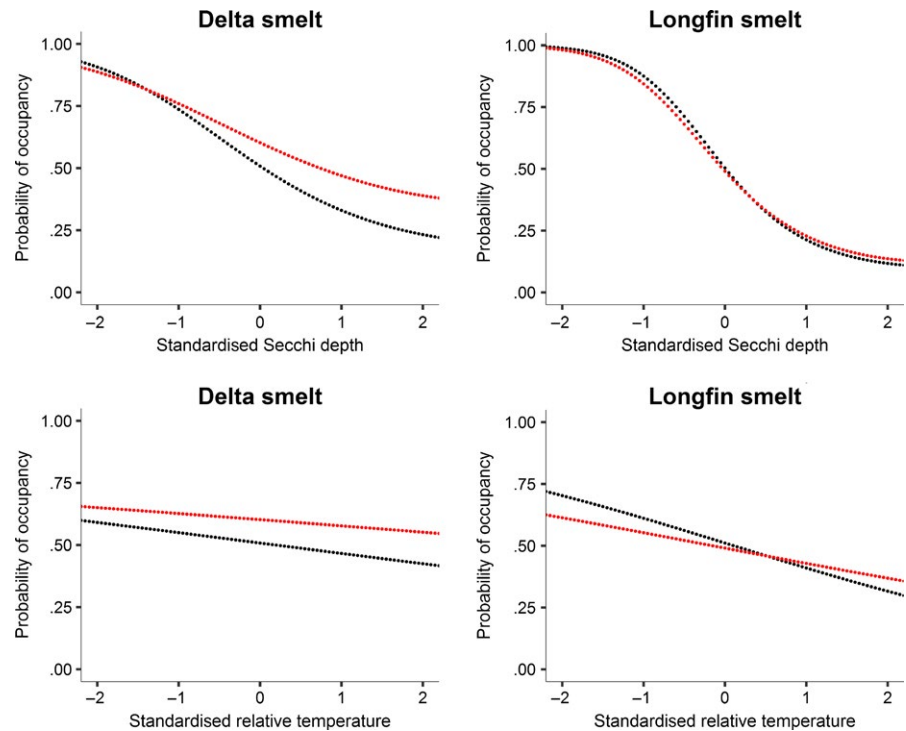


FIGURE 6 Model-averaged predictions for occupancy in relation to turbidity and temperature based on the top-ranked single-season models (black dotted lines) and spatial dependence models (red dotted lines). Median value inputs were used for continuous variables, while the year 1996 and ebb tide were used for categorical variables. [Colour figure can be viewed at wileyonlinelibrary.com]

Rose, Kimmerer, Edwards & Bennett, 2013a,b). For example, in warm and dry years that are typically associated with lower numbers of delta smelt (Feyrer et al., 2011; IEP MAST 2015; Moyle et al., 2016), an increase in the number of replicate tows can be planned ahead of time. Nevertheless, such adjustments to the monitoring programme's sampling effort would be contingent on multiple factors. Monitoring programmes, such as the 20-mm Survey, would need to consider the sampling mortality of fishes, permit limitations ("take"), processing time, cost and other logistical constraints. One potentially effective approach would be to increase sampling when the abundance level is expected to be low, but discontinue additional effort at that particular site after delta smelt is detected (MacKenzie et al., 2006). Moreover, regions in which presence/absence information is particularly crucial can be targeted specifically for increased number of replicate tows rather than a broad overall increase in sampling effort for the monitoring programme. New, non-lethal methods for detecting delta smelt can also be used in conjunction to increase detectability, such as the use of remote videography (Feyrer et al., 2013) or sampling of water for environmental DNA (Dejean et al., 2012; Ficetola, Miaud, Pimpanon & Taberlet, 2008).

4.3 | Environmental drivers of occupancy and detection probability

Understanding factors that influence a species' occurrence within the context of imperfect detection can provide insights into the species' ecology and the sampling method used. Despite the evidence of overdispersion in the single-season occupancy models, there appears to be few major differences between the general results of the single-season models and the spatial dependence models.

Consistent with what is known about delta smelt, longfin smelt and striped bass spawning dates (Moyle, 2002), the signs of day-of-year coefficients in the best occupancy models suggest that the 20-mm Survey in spring and early summer generally started prior to the annual spawning of striped bass but after the spawning of most longfin smelt.

All three species responded similarly to turbidity, with occupancy probability increasing with higher turbidity (i.e. lower Secchi depth). However, it is particularly important to note that longfin smelt occurrence was found to be as closely linked to turbidity as the delta smelt (Figure 6). While the strong positive association between delta smelt and turbidity has been well examined (Feyrer et al., 2007; Hasenbein, Komoroske, Connon, Geist & Fangue, 2013; Nobriga et al., 2008; Sommer & Mejia, 2013), past studies on longfin smelt have mainly focused on the species' abundance changes in response to freshwater flow (Nobriga & Rosenfield, 2016; Rosenfield & Baxter, 2007; Stevens & Miller, 1983). The association between juvenile longfin smelt and high turbidity indicate that the long-term turbidity decline in the Delta (Hestir, Schoellhamer, Greenberg, Morgan-King & Ustin, 2016; Schoellhamer, Wright & Drexler, 2013) may have negatively affected the species.

Relationships between temperature and occupancy vary by species. Young-of-year striped bass were not strongly associated with the existing spring and early summer temperature variation in the SFE (Tables 3, 4 and Tables S4, S6), but both smelt species occurred more often at locations with lower spring and summer temperature. Although both smelt species seem to be associated with lower temperature, longfin smelt occupancy at higher temperatures is predicted to be lower relative to delta smelt at higher temperature (Figure 6). This suggests that juvenile longfin smelt may be less tolerant of high



temperatures than delta smelt, a result consistent with laboratory studies (Jeffries et al., 2016).

This study did not evaluate all potential environmental variables that may predict the occupancy of these three fish species, including factors such as food availability, water velocity, contaminant exposure, or channel configuration, all of which can be key habitat features (Sommer & Mejia, 2013). Indeed, the overdispersion of the single-season model may be partially due to the exclusion of some of these potentially important habitat parameters. Nonetheless, the chosen variables are commonly regarded as major components of juvenile fish habitat in estuaries (Cyprus & Blaber, 1987; Feyrer et al., 2007, 2011; Gunter, 1961; Mac Nally et al., 2010) and understanding how these variables affect the species can inform management about contributing factors in their decline and future population trajectories.

In addition to parsing out some of the environmental factors affecting species' occupancy, the size selectivity of the gear used in the 20-mm Survey was also evaluated. Detection probability rarely remains constant, even when considering a single species within a season (MacKenzie & Kendall, 2002; Royle & Nichols, 2003). Detection probability for larval fish can be low early in the spawning season due to lower densities, peak at a certain time point and decline again as juvenile fish become scarcer due to mortality and gain the ability to avoid the net. The single-season occupancy models approximated the fish size in which detection probability reached its highest for each species. The highest detection probability for delta smelt was estimated to be approximately 25 mm FL, while peak detections for longfin smelt and striped bass were estimated to be approximately 14 mm FL (Figure 4). In contrast, the spatial dependence models seem to have overestimated the detection probability of the 20-mm Survey gear as the models predicted near perfect detection probability for larger sized delta smelt and smaller sized longfin smelt and striped bass. Although conducting new studies specifically aimed at addressing size selectivity can and should be carried out to acquire more precise estimates of gear bias (Myers & Hoenig, 1997; Newman, 2008; Stewart, Walsh, Reynolds, Kendall & Gray, 2004), results from this study illustrate the ability of an existing long-term data set to assess within-season heterogeneity in detection probability.

4.4 | Temporal trends in occupancy and detection probability

Although abundance indices for delta smelt, longfin smelt and striped bass have shown interannual fluctuations in the past, these species have declined significantly in the last decade (Sommer et al., 2007; Mac Nally et al., 2010; Thomson et al., 2010; IEP MAST 2015). A corresponding decline in general distribution for delta smelt and striped bass (based on occupancy estimates) was observed over the course of the study period (1995–2015) even after adjusting for imperfect detection. The exception was longfin smelt, where no clear trend was found using Mann–Kendall's tau test. The absence of a strong declining trend in longfin smelt occupancy is unexpected given their decline

in abundance over the past two decades (Rosenfield & Baxter, 2007; Sommer et al., 2007). The lack of a declining trend observed in this study is possibly due to some mismatch in the timing and location between the longfin smelt spawning season and the 20-mm Survey. For example, there is insufficient sampling of locations downstream of San Pablo Bay by the 20-mm Survey, where young-of-year longfin smelt are often abundant during high outflow years (Armor & Herrgesell, 1985; Feyrer et al., 2015; Rosenfield & Baxter, 2007). The later start dates for the 20-mm Survey in the late 1990s may also play a role in the data set's inability to detect a declining trend for longfin smelt occupancy, as the spawning season for longfin smelt generally starts in February (Moyle, 2002).

5 | CONCLUSIONS

This study highlights the utility of accounting for imperfect detection in a long-term, large-scale monitoring programme. Information on how species' life history and size affect detectability can be used to improve quantitative and conceptual models for species of conservation concern. Currently, such models are a major research focus for delta smelt (Nobriga et al., 2008; Feyrer et al., 2011; Rose et al., 2013a,b; Sommer & Mejia, 2013; IEP MAST 2015), although sampling precision and accuracy remain an ongoing issue due to the increasing rarity of this species. Monitoring programmes with a stated goal of assessing fish abundance and distribution should be aware of the potential increase in their false-negative error rate as abundance declines and programmes should attempt to quantify this imperfect detection when possible. Furthermore, given sufficient information on what predicts the species' abundance, monitoring programmes should consider adaptively managing their effort to account for the changing abundance and, thus, detectability of target species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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