Title
The Distribution and Abundance of Striped Bass and Other Estuarine Fishes in the San Francisco and Umpqua River Estuaries

Author
Stompe, Dylan Keating

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The Distribution and Abundance of Striped Bass and Other Estuarine Fishes in the San Francisco and Umpqua River Estuaries

By

DYLAN KEATING STOMPE
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Approved:

John Durand, Chair

Peter Moyle

Andrew Rypel

Committee in Charge

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Abstract

Fishes are highly important recreational, commercial, cultural, and food resources throughout the world. Of all fishes, estuarine fishes are perhaps the most accessible to humans and highly impacted by development and exploitation due to their proximity to major ports and centers of development. As a result, many populations of estuarine fishes have experienced drastic declines in abundance and shifts in distribution. This is especially true for the fishes of the San Francisco Estuary (SFE), which have had to contend with stressors in the form of waterway channelization, floodplain and marshplain "reclamation", aquatic toxicants, overexploitation, major shifts in hydrologic regimes, and the export of large quantities of freshwater from both riparian and appropriative water users. In response, numerous agency and university long-term monitoring programs have been established to monitor and inform the management of estuarine fishes in this system.

These monitoring programs have documented the precipitous decline of several fish species in the SFE. Of these species, striped bass are unique and contentious. Introduced to the SFE in 1879, striped bass soon colonized several other Pacific Coast estuaries, including the Umpqua Estuary in southern Oregon. In the century following their introduction, striped bass were heralded as a locally important recreational and commercial species, with much management focused on the persistence of their fisheries. In more recent history, they have been less highly regarded by management agencies, owing to their trophic positioning as a piscivore and their perceived impact on native fishes. Regardless of their perception as a predator, striped bass still represent productive recreational fisheries and play an important role as an indicator of estuarine "health."

My dissertation investigates the changes in abundance and distribution of juvenile striped bass and several other estuarine species, including Delta smelt, longfin smelt, and American shad. In addition, I investigate the current distribution of subadult and adult striped bass in the Umpqua Estuary. The analysis of estuarine fishes in the SFE starts with the integration of 14 long-term monitoring datasets and a cursory analysis of abundance in Chapter 1. This is then followed by a spatiotemporal analysis of abundance and distribution trends of striped bass and other estuarine fishes using generalized linear mixed models in Chapter 2. Finally, the investigation of subadult and adult striped bass distributional patterns is conducted using laser-ablation plasma mass spectrometry of striped bass otoliths to determine movement in relation to water isotopic signatures in Chapter 3.

Through my analyses I demonstrate the utility of integrated datasets and produce a dataset and web application for other researchers to utilize. I also show a decline in abundance and a change in the distribution of striped bass as well as several other estuarine fishes in the SFE. The distribution of these fishes has constricted considerably, with the Central and South Delta largely devoid of iconic estuarine fishes once common throughout the SFE. Finally, I show that striped bass are both present and actively reproducing in the Umpqua River Estuary, with no evidence of immigration from the SFE.

Chapter 1

Comparing and Integrating Fish Surveys in the San Francisco Estuary: Why Diverse Long-term Surveys are Important

Dylan K. Stompe[1]

Peter B. Moyle[1]

Avery Kruger[1]

John R. Durand[1]

Affiliation

[1]*Center for Watershed Sciences, University of California, Davis, Davis CA 95616 USA*

Abstract

Many fishes in the San Francisco Estuary (SFE) have suffered declines in recent decades, as shown by numerous long-term monitoring programs. These programs have produced rich datasets that are useful for tracking species trends over time. Problems arise from drawing conclusions based on one or few surveys, because each survey samples a different subset of species and/or reflects different spatial or temporal trends in abundance. The challenges in using these datasets for comparative purposes stem from methodological differences, magnitude of data, incompatible data formats, and end-user preference for familiar surveys. To improve survey utility and encourage multi-survey analyses, we quantitatively rate surveys based on their ability to represent species trends, present a methodology for integrating long term survey data, and provide examples that highlight the importance of expanded analyses. We identify areas and species that are under-sampled and compare fish salvage from large water export facilities with survey data. Our analysis indicates that while surveys are redundant for some species, no two surveys are completely duplicative. Differing trends become evident when considering individual and aggregate survey data, implying spatial, seasonal, or gear dependent catch. Our quantitative ratings and integrated dataset allow for improved and better-informed comparisons of species trends, while highlighting the importance of the current array of sampling programs.

Introduction

The San Francisco Estuary (SFE) is an anthropogenically altered, geographically complex estuary that drains a watershed of more than 194,000 square kilometers in northern California (Conomos et al. 1985). Historically, the SFE supported productive commercial and recreational fisheries for both native and introduced species (Scofield 1931; Yoshiyama et al. 1998). Rapid human population growth and increasing demands for water resulted in overharvest of many fish species, invasions of non-native species, and widespread habitat alteration (Nichols et al. 1986; Cloern and Jassby 2012). These factors in turn led to the decline of some native and long-established non-native species, as well as some extinctions (Kohlhorst 1999; Moyle 2002, Sommer et al. 2007).

To document the status of important SFE fish species, numerous agency and university surveys were established between 1959 and present, of which at least 14 have operated continuously for 17 years or more (Table 1.1, Appendix Table 1.1). Survey methods include a variety of trawls, beach seines, gill nets, and fyke traps. Most surveys were initiated to track either juvenile Striped Bass (*Morone saxatilis*) or juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) abundance. Since their inception, many have shifted emphasis to Delta Smelt (*Hypomesus transpacificus*) and other endangered species. Methodologies remained largely consistent and survey crews generally recorded all species captured, resulting in a long record of fish abundance and diversity.

The challenges in using these datasets for comparative purposes result from the magnitude of data from each survey paired with incompatible data formats (i.e. species coding, units, file type, etc.). Problems arise in drawing conclusions based on one or few surveys, because each survey samples a different subset of species and/or reflects different spatial or temporal trends in abundance. Because of disparate data formats and species coding, researchers and managers rarely conduct analyses across the breadth of datasets. We identified these issues through our own exploratory analysis of SFE species trends across surveys, which proved difficult and time-consuming.

Here, we compare relative catch of different fish species and assemblages across 14 SFE surveys, and then provide methods to integrate survey datasets for analysis of broad species trends. We use the integrated dataset to provide examples of disparities in survey catch for select species and to make comparisons of survey results with fish salvage data (referred to hereafter as 'salvage') from the State Water Project (SWP) and Central Valley Project (CVP) export pumps in the South Delta. Comparisons were made with salvage data to explore the utility of this data-rich, yet often overlooked, resource to estimate fish abundance. Finally, we selected a subset of SFE surveys that can be easily compared because of consistency of effort over time. We use these to evaluate long-term species trends of four important fish species identified with the Pelagic Organism Decline (POD, Sommer et al. 2007). Our study should complement recent work that the Interagency Ecological Program has taken towards making SFE datasets more readily accessible.

To integrate datasets, we reformatted fish and water quality data to provide consistency across all surveys. Patterns derived from the integrated dataset are valid at population-scales and can be used to compare relative abundance of fish caught in each survey. Integrated data allow basic questions posed by managers to be answered quickly and efficiently, and results can suggest the need for further in-depth analysis. For example, Dahm et al. (2019) used an early version of our approach of identifying relative survey selectivity to suggest improved monitoring in the Delta by using whole fish assemblages rather than just endangered native fishes. To demonstrate the utility of the integrated data we address the following questions:

- How much redundancy is there among surveys?
- What areas and species are inadequately sampled?
- What are the abundance trends amongst POD species across surveys?

- Are salvage data consistent with other surveys?

Methods

We evaluated and integrated the data from 14 surveys in a series of steps. First, we estimated which species and assemblages were best represented in the surveys, producing what we termed “Species-Survey Ratings”. We then combined the data from these surveys into one, open-access dataset with associated water quality and catch data, which we call the “SFE Integrated Dataset” (SFE ID). Using the SFE ID, we compared differences in catch of POD species among all surveys as well as salvage. Finally, in order to more confidently evaluate species trends across multiple surveys, we used a subset of surveys from the SFE ID that were most comparable in terms of longevity and consistency of effort. The resulting eight surveys were combined into what was termed the “SFE Survey” (SFES) and used to evaluate trends in POD species abundance.

Species-Survey Ratings

As an exploratory effort to quantify which individual survey data were best suited for analysis of trends in species abundance, we constructed an equation to rate species-survey relationships. We developed these ratings using the equation:

$$R^2 = \frac{f_{sp}}{n} \sqrt[3]{\frac{T_c}{M_c}} \qquad \text{(Eq. 1)}$$

where “R” represents the species-survey rating, “f_{sp}” is the number of years in which a given species was caught in the survey, “n” is the total number of years in which a survey has operated, “T_c” is the total catch of a given species over the life of the survey, and “M_c” is the total catch of the most caught species over the life of the survey. R-values were calculated for 36 species (Appendix Table 1.2) that were selected based on current or historical prevalence within the Delta (Dahm et al. 2019; Table 1.2). Higher R-values indicate better species representation in the survey. Newer SFE surveys were omitted because of limited data but they will become increasingly useful as their durations increase.

Equation 1 was constructed iteratively to maximize spread of R-values between zero and one. The first portion of the equation (f_{sp}/n) penalizes surveys that do not consistently catch a species while the second portion ($\sqrt[3]{(T_c/M_c)}$) standardizes catch in relation to the maximum individual species catch for a given survey. The square and cube root portions of the equation are applied so that highly abundant species, such as Threadfin Shad (*Dorosoma petenense*), do not overwhelm those species which exist at intrinsically lower population levels. An R-value of one corresponds to the species which has been caught in the highest cumulative numbers and frequency for a given survey and a zero corresponds to any species which was not caught over the life of a given survey.

We also evaluated selectivity of surveys for certain fish assemblages (Pelagic, Benthic, Fringe, Submerged Aquatic Vegetation [SAV]; Appendix Table 1.2). Mean R-values per assemblage for all surveys and salvage were used to compare overall relative sampling selectivity of assemblages (Table 1.3).

SFE Integrated Dataset

Data from the surveys in Table 1.1 were used to create the SFE Integrated Dataset (SFE ID). Data were sourced from the California Department of Fish and Wildlife (CDFW) file transfer protocol 'FTP' server (CDFW 2019), the Environmental Data Initiative (EDI) data portal (Mahardja and Speegle 2018; Schreier et al. 2018), and through data requests from university personnel (O'Rear et al. 2019). All fish species captured were included. Once aggregated, data were read into the program R and reformatted and restructured into a compatible format to allow datasets to be joined (R Core Team 2019).

Reformatting and restructuring for compatibility involved renaming species using CDFW Bay Study Survey species code conventions (six letter coding), renaming columns for environmental variables, and casting data into a horizontal format. Environmental variables retained for the SFE ID include water temperature, water depth, Secchi depth, and salinity. Data records are incomplete for water depth and salinity, but water temperature and Secchi depth are consistent. Year, date, time of sampling, method, survey, station name, and station coordinates were also included.

Many surveys report their findings through unique indexing methods, such as reporting catch per area or volume of water sampled. Given the differences in area sampled and catch efficiency among gear types, in addition to the fact that not all surveys report volume or flowmeter readings, we chose not to index catch against volume sampled. Instead, we report catch per unit effort (CPUE) of all surveys as catch per trawl/seine. Similarly, rather than index salvage catch against volume of water exported, we treated salvage CPUE as catch per day. Our approach with these data does not allow for direct catch comparisons between surveys and/or salvage due to differential gear efficiencies. However, it does provide an accessible aggregative dataset that can be cautiously analyzed while recognizing the potential comparability issues associated with our methodological decisions. Full R code for dataset integration is available in the supplemental materials.

Using the SFE ID, we visualized sampling distribution and species trends. Current sampling distribution for the 14 SFE ID surveys (2017) was plotted as a heatmap (Figure 1.1). We then visualized differences in trends for fishes identified in the POD as mean yearly CPUE across all 14 surveys (Figure 1.2). Species of the POD are Striped Bass, Threadfin Shad, Longfin Smelt (*Spirinchus thaleichthys*), and Delta Smelt. We also visualized CPUE of Sacramento Splittail (*Pogonichthys macrolepidotus*), a species native to the SFE which appears to have maintained a healthy, if isolated, population (Sommer et al. 1997; Moyle et al. 2004, 2020).

Through coding in program R (Chang et al. 2018; R Core Team 2019), we created a Shiny application that allows for simple exploratory visualization of temporal and spatial species trends using the SFE ID. Data filtering tools were added to aid in survey comparison and plots and data can be downloaded directly from the application. This application is published on the internet and can be accessed by researchers, managers, and the public.

Delta Salvage

To understand whether salvage tracks species abundance trends, we compared mean annual CPUE for the POD species among four key surveys and salvage using a scatterplot matrix (Figure 1.3). Within the scatterplot matrix, we plotted relative density as the number of observations of mean annual catch for each survey and species (Figure 1.3). We also tested the relationship in POD species mean annual catch between surveys and salvage using Spearman rank correlation. Spearman rank correlation was chosen in order to describe non-linear relationships given that surveys and salvage catch may scale differently under different environmental and operational conditions. Correlations of individual species are color coded, while the correlation of all POD species combined is given in black (Figure 1.3).

SFE Survey and POD Species Trends

By considering surveys in aggregate, we can increase the effective sample size and spatial extent compared to a single survey analysis. To increase comparability of SFE ID data, we created a subset of SFE ID surveys that have continuously operated since 1980, which we combined as the SFES. The continuous surveys include the CDFW Summer Townet Survey, CDFW Fall Midwater Trawl Survey, CDFW Bay Study Midwater and Otter Trawl Surveys, UC Davis Suisun Marsh Otter Trawl and Beach Seine Surveys, US Fish and Wildlife Service (USFWS) Beach Seine Survey, and the USFWS Chipps Island Midwater Trawl Survey. We only included continuously sampled stations between 1980 and 2017 (n=221). We constrained the Fall Midwater Trawl Survey to September through December and Chipps Island Midwater Trawl Survey to April through June for consistency because these two surveys have historically expanded and contracted their sampling efforts between years.

As a final measure to increase the validity of trends identified using the SFES, we controlled for changes in annual sampling intensity by equally weighting each of the eight surveys. Surveys were equally weighted by averaging the mean CPUE of each survey by year. This was done because while spatial and temporal variability had been constrained, there was considerable variability in sampling intensity between years for the Chipps Island Trawl Survey and USFWS Beach Seine Survey. Equally weighting surveys produces a metric of annual CPUE in which aggregate gear efficiency does not change over time.

To explore the utility of the SFES dataset and examine difference in trends of POD species, we plotted stacked bar graphs of mean yearly CPUE values using the SFES and Fall Midwater Trawl Survey data (Figure 1.4).

Results

Species-Survey Ratings

Through coding in program R (R Core Team 2019), we quantitatively rated 14 surveys using equation 1 to calculate R-values for each survey across 36 Delta species. The quantitative ratings are presented in Table 1.2, showing the relative selectivity of surveys for Delta fishes. No two surveys had the same rank order of species R-values, and most of the 36 Delta species showed high catches in at least one survey (Table 1.2).

This table shows that while species may be well represented in some surveys, they may also be nearly or totally absent in others. For example, Mississippi Silverside (*Menidia audens*) is the most frequently caught species in the three beach seine surveys, and nearly the most caught species in the Mossdale Kodiak Trawl Survey, but it is mostly absent from the two Bay Study surveys, and only marginally represented in the Fall Midwater Trawl Survey, Sacramento Midwater Trawl Survey, and Chipps Island Midwater Trawl Survey (Table 1.2). Similarly, Sacramento Splittail are well represented in the Mossdale Kodiak Trawl Survey and Suisun Marsh Otter Trawl Survey, but relatively poorly represented in the Sacramento Kodiak Trawl Survey (Table 1.2).

When mean R-values by assemblage are considered (Table 1.3), Pelagic species (R = 0.56) are most well represented across all the surveys, followed by Fringe and Benthic species (R = 0.26 and 0.25, respectively); SAV-oriented species were the least well represented (R = 0.20).

Similar to Table 1.2, individual survey R-values are not in total agreement across assemblage groups and agreement by gear type is mixed. For example, R-values dictate that the Yolo Bypass Beach Seine Survey is most effective at capturing SAV oriented fishes, while a survey with similar gear type, the Suisun Marsh Beach Seine Survey, has a very low R-value (R = 0.06) for the same assemblage group. Conversely, the two surveys using otter trawls, the Bay Study Otter Trawl Survey and Suisun Marsh Otter Trawl Survey, were both more effective at sampling benthic fishes than any other gear type (Table 1.2).

SFE Integrated Dataset

We successfully integrated 14 SFE surveys into the SFE ID. The SFE ID is organized horizontally, with each row representing a single trawl or seine pull. Survey identifier and method columns allow for discrimination of catch by survey and gear type, across the 167 fish species which have been captured by the 14 surveys. Of these 167 fish species, 120 have been captured at least ten times (Appendix Table 1.3). While some recorded environmental variables differ and were omitted (channel vs. shoal, presence of debris, weather, etc.), major water quality metrics such as water temperature, water depth, Secchi depth, and salinity were consistently recorded by most of the surveys and are included in the SFE ID. The SFE ID in .csv format and the code associated with its construction can be downloaded from the supplemental material or by request from the corresponding author. In addition, a program for exploratory visualization of these data can be found at the following link: https://baydeltalive.com/fishsurveystudy/fish-survey-study.

Using the stations that are currently sampled by the surveys of the SFE ID, we mapped the density of stations as a metric of sampling intensity (Figure 1.1). This figure shows that the majority of sampling stations are clustered in the southern and eastern portions of San Pablo Bay, Suisun Bay and Suisun Marsh, and along the Sacramento River corridor of the western Delta. Conversely, southern San Francisco Bay, northern San Pablo Bay, and the central and southern Delta are relatively sparse in their number of currently operating sampling stations.

Mean annual catch of the four POD species and Sacramento Splittail show disparities in trends amongst the 14 surveys of the SFE ID (Figure 1.2). For example, if we examine trends in Threadfin Shad mean annual catch, the Suisun Marsh Otter Trawl Survey (SOT), Suisun Marsh Beach Seine Survey (SBS), Bay Study Midwater Trawl Survey (BMW), and the Mossdale Kodiak Trawl Survey (MKT) would all seem to indicate that populations have trended positive since the year 2000, when POD was identified using the Fall Midwater Trawl Survey (FMW). In fact, the Twenty Millimeter Trawl Survey (TTN) and USFWS Beach Seine Survey (UBS) had some of their highest mean annual catches of Threadfin Shad during the time period identified as the POD. Similarly, mean annual catch of Sacramento Splittail has steadily increased since approximately 1990 in the Suisun Marsh Beach Seine (SMS) and Otter Trawl Surveys (SOT); a trend not seen in any other survey of the SFE ID.

Delta Salvage

The R-values for a majority of species captured in the salvage facilities are high, and all species were captured except for Spotted Bass (*Micropterus punctulatus;* Table 1.2). In contrast to the majority of other surveys, most species are at least moderately well represented by salvage, and only five species have an R-value of less than 0.2 (Table 1.2). This evenness is apparent when considering species assemblages as well and is only surpassed by the USFWS

Beach Seine Survey and Yolo Bypass Beach Seine Survey when measured as the difference between the best represented and least represented assemblage group (Table 1.3).

When salvage is compared to a subset of SFE ID surveys, correlation of mean annual catch between salvage and the surveys appears to be no more variable than correlation between surveys. For example, mean annual salvage of Striped Bass is strongly correlated with mean annual catch by the Summer Townet Survey (STN) (cor = 0.68) and the Fall Midwater Trawl Survey (FMW) (cor = 0.60; Figure 1.3). While this is a lower level of correlation in mean annual catch of Striped Bass than between the Fall Midwater Trawl Survey (FMW) and Summer Townet Survey (STN) (cor = 0.895), it is considerably higher than the correlation between the Fall Midwater Trawl Survey (FMW) and USFWS Beach Seine Survey (UBS) (cor = 0.02; Figure 1.3). This incongruity in correlation of POD species catch remains constant across the surveys included in Figure 1.3.

Similarly, we may examine the density of POD species catch for salvage and the subset of SFE ID surveys in Figure 1.3 as a means of investigating their agreement with one another. The plots running diagonally in Figure 1.3 represent the density of observations of annual catch, with the x-axis corresponding to the number of a given species caught per year and the y-axis the number of observations. Given this, species that are caught in high numbers in a given survey will be clustered around the right side of a plot and low catch on the left side of a plot. Species which are caught in consistent numbers will be represented by a single peak in the density plot, whereas species with a high annual variability in catch will have a lower peak and wider density distribution.

Using the density plots, we can see that salvage catch of Threadfin Shad and Striped Bass is consistent and in high numbers (Figure 1.3). This is supported by R-values, which identify

Striped Bass and Threadfin Shad as the two most well represented species in the salvage data (Table 1.2). The Suisun Marsh Otter Trawl Survey, which also has a high peak in mean annual Striped Bass density of catch, has low correlation in catch with salvage (cor = 0.09; Figure 1.3).

SFE Survey and POD Species Trends

We increased the validity of considering SFE ID surveys in aggregate by turning a subset of the SFE ID datasets into the SFES dataset. This dataset includes only surveys that have run consistently since 1980 and has been spatially constrained to only include continuously operated stations and temporally constrained to consistent seasonal periods. Our subsetting and filtering procedures resulted in an aggregate dataset that can be leveraged to analyze SFE species trends with considerably expanded seasonal and spatial coverage.

Through equal weighting of annual SFES survey catch data, we analyzed trends in POD species abundance in comparison to trends identified using the Fall Midwater Trawl Survey (Figure 1.4). We show that the POD decline around the year 2000 is far less pronounced when the SFES is compared to the Fall Midwater Trawl Survey. For example, Threadfin Shad, which shows a dramatic decline after the year 2000 in the Fall Midwater Trawl Survey, remains at relatively stable population levels before and after the start of the POD when SFES data is considered (Figure 1.4). Striped Bass, which also shows a decline around the year 2000 in the Fall Midwater Trawl Survey, seem to remain at relatively stable population levels between the mid 1980s and present when looking at the SFES data. The trends shown by the SFES are in general agreement with the Fall Midwater Trawl Survey when the two smelt species are considered. However, the decline around the year 2000 appears to follow a slight rebound in 1993 after a period of drought, rather than being a prolonged decline (Figure 1.4). It would appear, based both on the SFES and Fall Midwater Trawl Survey datasets, that the principal decline in Delta Smelt, Longfin Smelt, and Striped Bass occurred in the early to mid 1980s, rather than around the year 2000 (Figure 1.4). This apparent decline in these three species occurred outside of a drought period and before the introduction of *Potamocorbula amurensis*, an invasive species and ecosystem engineer that has often been credited with driving native species decline in the SFE (Mac Nally at al. 2010, Thomson et al. 2010).

Discussion

Researchers and managers often choose one or a few surveys based on preference or convention when tasked with describing particular species abundance trends or implementing environmental regulations (Sommer et al. 2007; Mac Nally et al. 2010; Thomson et al. 2010; Frisch et al. 2011; Miller et al. 2012). However, the R-values from our Species-Survey Ratings show differences in selectivity (Table 1.2); this is likely a result of gear type, sampling sites, and seasonality. For example, surveys that sample with midwater trawls preferentially capture pelagic species, whereas otter trawls were relatively more effective at sampling benthic species. Identification of species selectivity by location and season are beyond the scope of this paper; however, this type of analysis will be possible using the SFE ID and SFES datasets.

Visualizations from the integrated dataset show that the single survey approach is not appropriate for many species (Figures 1.2-1.4). For example, while the POD is evident from the Fall Midwater Trawl Survey data, it appears to be muted when considering the aggregated SFES dataset (Figure 1.4). Acknowledging these disparities is important in the management of the SFE, given the richness of available data and investment of resources in mitigation and restoration. Even a survey that produces high quality data on diverse species, such as the Fall Midwater Trawl Survey, cannot adequately capture all trends in species abundance.

The Species-Survey rating table (Table 1.2), when combined with simple plots of CPUE trend data and survey spatial extent, allows for a first cut at looking at trends in all species, across surveys. Given the enormous differences in sampling gear among surveys, lengths of the sampling programs, diversity and number of sampling locations, and annual timing of surveys, there may be limitations to this analysis. Nevertheless, the data can be used to answer questions such as:

Is there high redundancy among surveys?

The SFE is most extensively surveyed for pelagic fishes (Table 1.3), with the greatest intensity of sampling being in the North Delta, West Delta, Suisun Bay, Suisun Marsh, and San Pablo Bay (Figure 1.1). Although some surveys have similar target species and regions, no one survey is entirely duplicative of another, because sampling occurs at different frequencies, locations, times of the year, and with different gear types (Appendix Table 1.1). Species found in large numbers in multiple surveys, such as Striped Bass and Threadfin Shad, do not show the same trends in abundance in all surveys (Figure 1.2-1.4). Likewise, trends in annual POD species CPUE vary among surveys (Figure 1.3). These instances highlight the importance of maintaining multiple sampling programs. Differences in survey catch may be due to poorly understood drivers such as changes in species distribution, behavior, or the characteristics of sampling stations (Schroeter 2008; Sommer et al. 2011). Surveys often track these changes differently based on unique responses to spatial, seasonal, or gear type differences. Monthly variation in effort is relatively evenly distributed, aside from an increase in effort during summer months. However, further analysis of the SFE ID is needed to truly disentangle seasonal effects on catch.

What areas and species are inadequately sampled?

Fishes associated with SAV, particularly in the southern and central Delta, are inadequately sampled (Figure 1.1, Tables 1.2 and 1.3). For example, Largemouth Bass (*Micropterus salmoides*) has low Species-Survey ratings (Table 1.2) even though it is known to be an abundant species within the southern/central Delta, where it supports an important recreational fishery. The low rating is likely because Largemouth Bass, as well as a suite of centrarchid species, are most commonly associated with environments dominated by submerged aquatic plants (Durocher et al. 1984), which are poorly sampled by the trawls and seines that are the most widely used survey gear.

Historically, there has also been poor survey coverage of northern San Pablo Bay as well as the central and southern portions of the San Francisco Bay. Newer surveys have increased coverage in some of these areas (UC Davis Otolith Geochemistry & Fish Ecology Laboratory) but were not included in our analyses due to limited temporal span. These fill some spatial gaps and will prove increasingly valuable in future datasets.

The poor representation of these areas and fishes in the surveys (except salvage and some beach seine surveys) is related to the initial purpose of most of the current sampling programs. Surveys were primarily started to track trends in abundance for Chinook Salmon and Striped Bass; these are species which are not associated with SAV and which occur primarily (at least as juveniles) in the corridor between San Pablo Bay and the Sacramento River. University and agency programs have conducted aperiodic surveys which effectively sample these fishes, mostly using electrofishing. However, these surveys have not operated continuously for long periods of time, limiting their usefulness in tracking species trends. The establishment of long-term monitoring of these fishes through appropriate sampling methods, such as boat electrofishing, would more adequately allow for tracking of populations of SAV associated fishes.

What are the trends in fish species identified as part of the pelagic organism decline (POD), in diverse surveys?

Exploratory analysis of POD species trends using the SFE ID and SFES datasets challenges some of the trends identified using the Fall Midwater Trawl Survey (Sommer et al. 2007). Threadfin Shad do not show the longer-term decline as is seen for other POD species that show declines beginning in the early 1980s, punctuated by brief, and slight, recovery in the early 1990s. The subsequent decline, identified as *the* POD (Sommer et al. 2007), is less dramatic using data from SFES as opposed to using data from just the Fall Midwater Trawl Survey (Figure 1.4). The timeline shown by the SFES is more consistent with known step-changes to the ecology of the upper estuary (Mac Nally et al. 2010, Thomson et al 2010), particularly after the invasion and spread of two ecosystem engineers; the benthic clam *Potamocorbula amurensis* in Suisun Bay (Carlton et al 1990, Nichols et al 1990) and the aquatic weed *Egeria densa* in the Delta (Durand et al 2016).

Do the salvage data show the same species trends as shown in surveys?

Salvage data should be used with caution due to the dependence of catch on variable pump operations; however, the richness of this dataset should not be overlooked. Salvage data for some species reflect abundance trends seen in other surveys, particularly for Delta Smelt and Striped Bass, which correlate well with Summer Townet Survey and Fall Midwater Trawl Survey data (Figure 1.3). This is potentially driven by the pelagic life history and (historically) estuary-wide distribution of these two species, making them vulnerable to capture both by surveys and salvage operation.

The results of our limited investigation into differences in salvage between SWP and CVP indicate that these two facilities may not return complimentary results. This may be due to differences in operation as well as the effects of predation in Clifton Court Forebay (SWP). Although high correlation exists between some surveys and combined South Delta salvage, caution should be exercised when considering SWP and CVP salvage data separately.

Conclusions

Our analyses demonstrate the necessity of using a suite of surveys to evaluate fish trends in the SFE. Using individual or aggregate survey data provides different lenses through which to view ecosystem dynamics, which are often cryptic. Because the SFE is a diverse and dynamic ecosystem, no single survey will adequately inform system-wide management needs or resolve scientific uncertainties. The species-survey ratings, data aggregation procedures, and the readily accessible SFE ID dataset, along with visualization software, allow researchers and managers to more fully exploit the breadth of sampling programs within the SFE. Given the increased spatial and temporal breadth of these data, researchers may more effectively identify long-term or broad spatial trends in abundance and distribution of SFE fishes. This will aid in the generation of hypotheses about the status and trends of fishes, both native and non-native, and will strengthen SFE management. We hope this exercise encourages survey managers to continue working to adopt universal procedures and coding, so as to facilitate future collaboration and dataset integration.

Our analysis of spatial and species coverage suggest that no two surveys are in agreement for all species, which suggests elimination of any survey should be done with great caution, especially when declining species are involved. In order to more holistically survey the estuary, sampling should be expanded beyond what is necessary to describe trends in listed species abundance. This is particularly true for under-sampled regions such as the southern Delta and southern San Francisco Bay, and for SAV-associated and marine fishes, which are poorly understood in the SFE and subject to accelerating change from global warming, water management, restoration practices and infrastructure development.

Our analysis identifies potential pitfalls of relying on limited data to inform system management. More intensive analyses should build upon the SFE ID to help identify drivers of differences in species trends, which may be hidden in the seasonal, spatial and environmental aspects unique to each survey. These drivers should be further analyzed both to reveal factors important to species management as well as to identify improvements that are needed to the sampling of fishes within the SFE.

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Figures

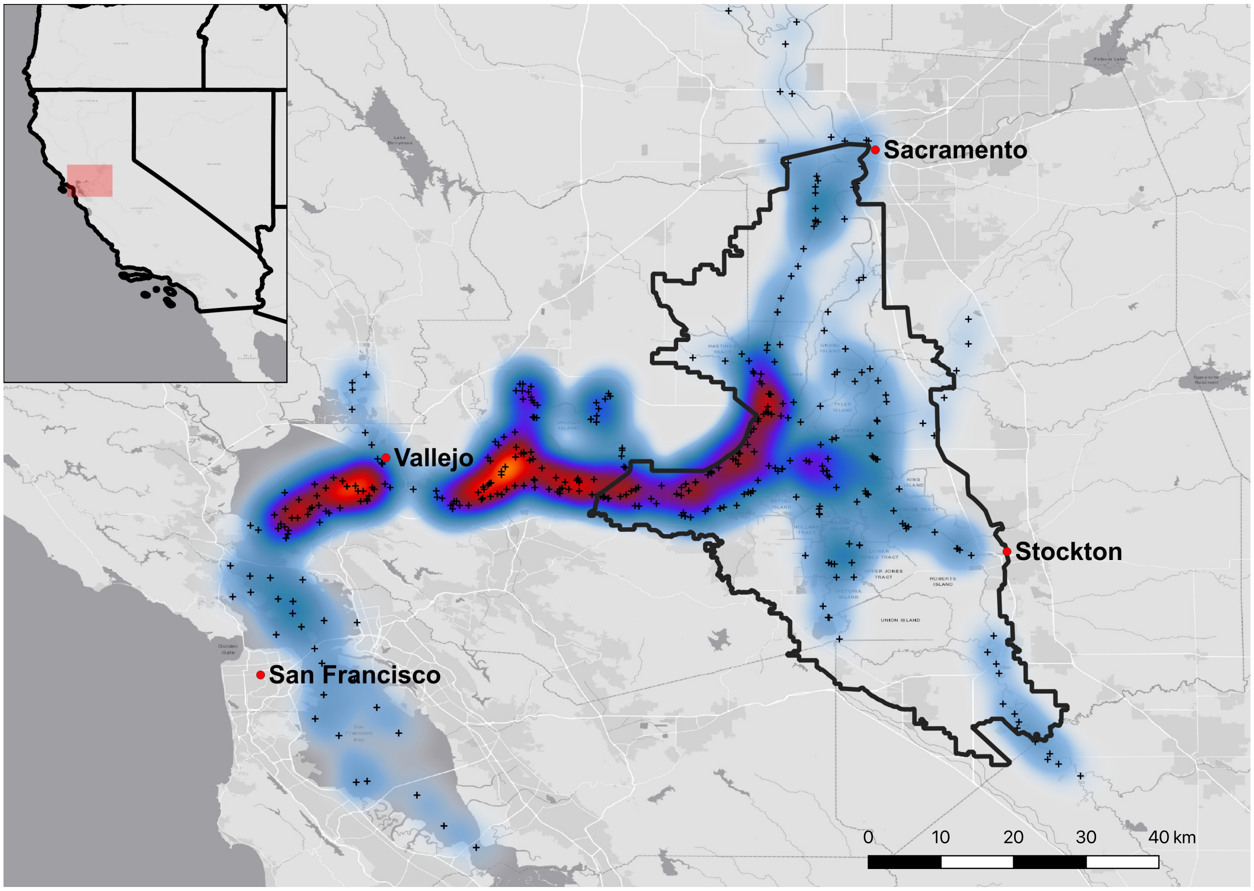

Figure 1.1. Heatmap of sampling intensity (by number of stations) across 14 surveys within the San Francisco Estuary. Only currently surveyed stations from SFE ID surveys are included. Black outline represents the legal Delta boundary and black crosshairs represent individual survey stations.

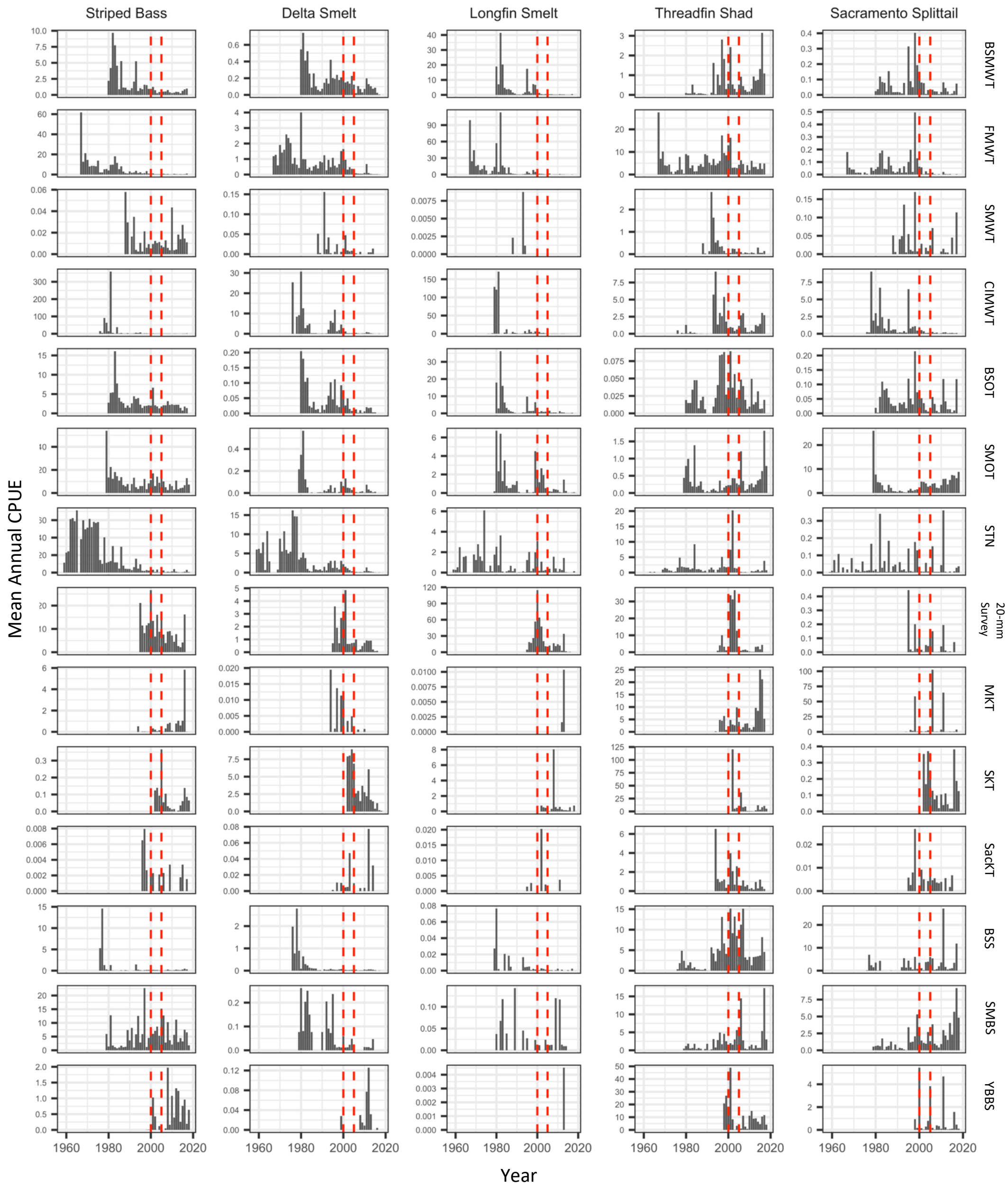

Figure 1.2. Mean annual CPUE of POD species (Striped Bass, Delta Smelt, Longfin Smelt, Threadfin Shad) and Sacramento Splittail across 14 SFE Surveys. CPUE calculated as either catch per trawl or catch per seine, depending on survey methods. Dashed vertical red lines represent the period of time identified as POD. Survey abbreviations in Table 1.1.

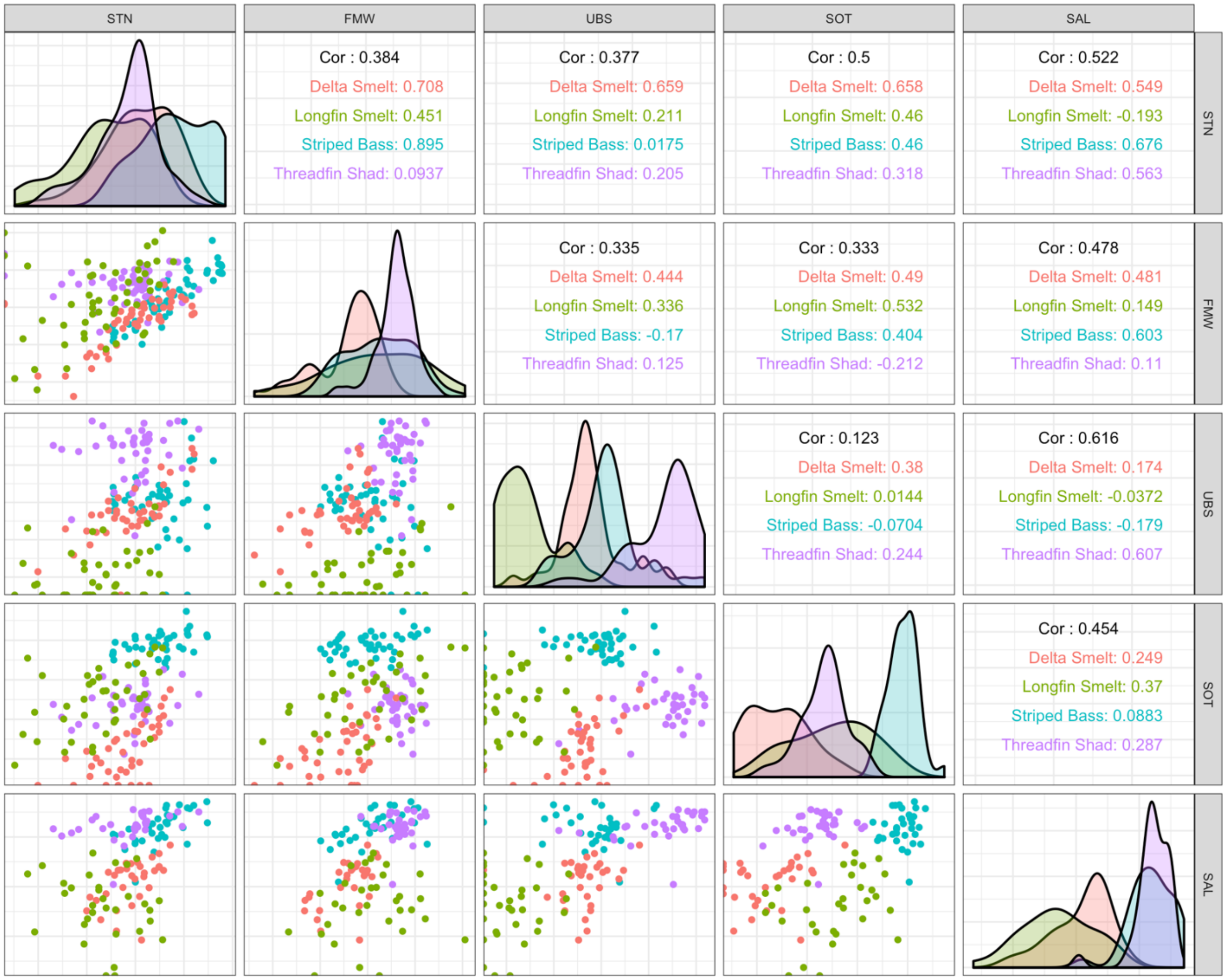

Figure 1.3. Scatterplot matrix of mean annual CPUE of POD species for four longstanding SFE surveys as well as South Delta Salvage. Lower left plots are CPUE relationships between surveys and/or salvage, diagonal are density plots of mean yearly CPUE for each survey and/or salvage, and upper right are Spearman rank correlations of CPUE between surveys and/or salvage. Species colors in upper right panels are the same as those used in scatter plots and density plots. See Table 1.1 for abbreviations. Scatterplot axes are on a log scale.

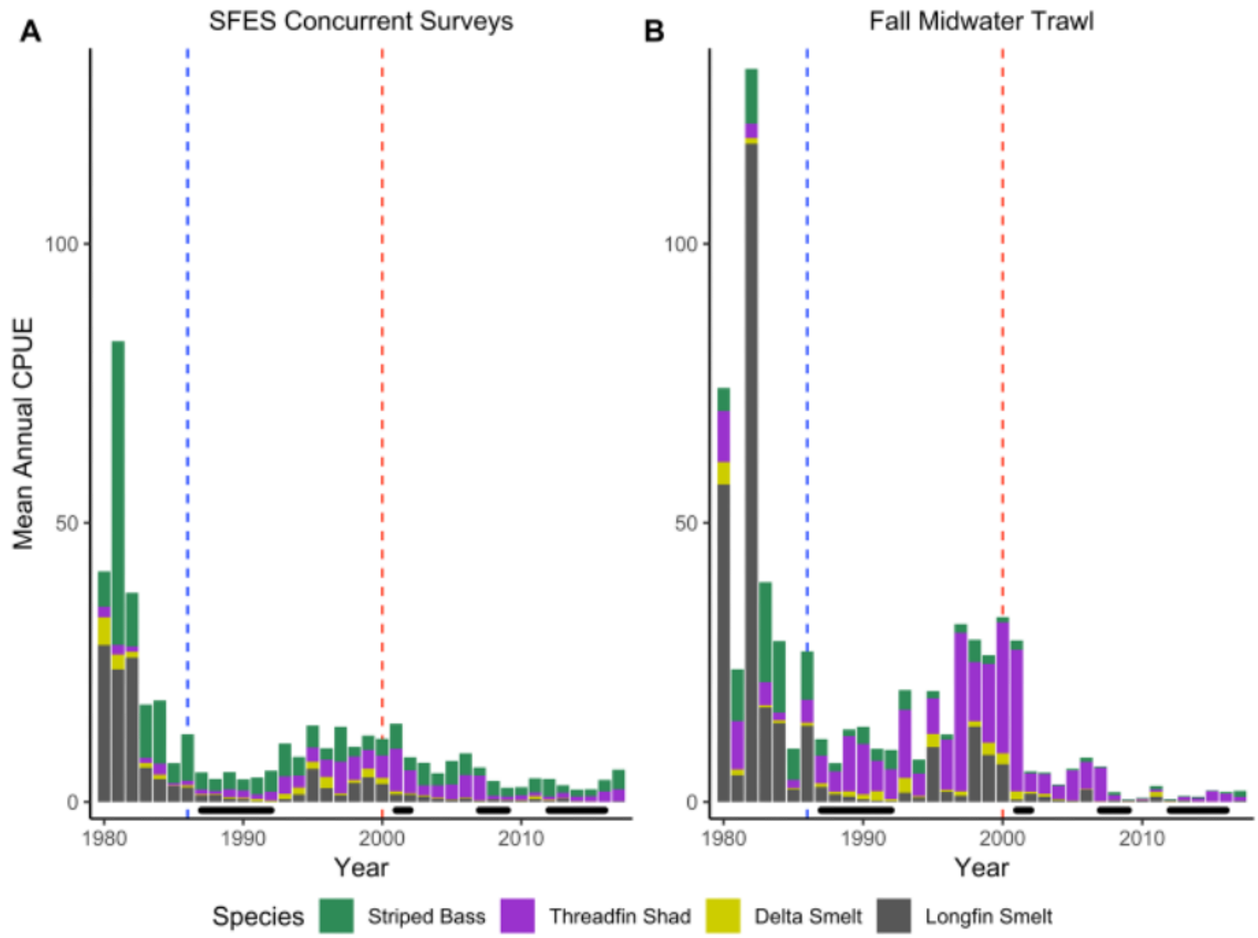

Figure 1.4. Stacked bar plot of mean annual CPUE of POD species between 1980 and 2017. Panel A was generated using continuously sampled stations (n=221) for concurrently operating surveys of the SFES (n=8) and panel B was generated using continuously sampled stations (n=88) of the CDFW Fall Midwater Trawl. Mean annual CPUE for SFES concurrent surveys was calculated as an average of mean survey CPUE. Vertical dashed red line (x=2000) represents the start of POD (Sommer et al. 2007), vertical dashed blue line (x=1986) represents the introduction of *Corbula amurensis*, and horizontal black lines represent major periods of drought.

Tables

Table 1.1. Long term fish monitoring surveys that encompass all or part of the SFE. They are briefly described in in Appendix Table 1.1. Most are also described in detail in Honey et al. (2004). Abbreviations assigned for use in integrated dataset and data visualizations. Last two letters of abbreviation refer to gear type – MW = midwater trawl, OT = otter trawl, TN = townet, KT = Kodiak trawl, BS = beach seine.

Agency	Survey	Abbreviation
CDFW	Bay Study Midwater Trawl	BMW
CDFW	Fall Midwater Trawl	FMW
USFWS	Sacramento Midwater Trawl	SMW
USFWS	Chipps Island Trawl	CMW
CDFW	Bay Study Otter Trawl	BOT
UC Davis	Suisun Marsh Otter Trawl	SOT
CDFW	Summer Townet	STN
CDFW	20mm Trawl	TTN
USFWS	Mossdale Trawl	MKT
CDFW	Spring Kodiak Trawl	SKT
USFWS	Sacramento Kodiak Trawl	UKT
USFWS	Beach Seine Survey	UBS
UC Davis	Suisun Marsh Beach Seine	SBS
DWR	Yolo Bypass Beach Seine	YBS

Table 1.2. Calculated species-survey rankings for 36 Delta species across 14 SFE surveys and the SWP South Delta salvage. Ranks calculated as "R" in equation 1. R values were conditionally formatted on a continuous scale from zero to one, with zero as white and one as dark green. The darker the green color, the more well represented the species was in the survey. Species ordered by habitat association (leftmost column) where B = benthic, F = fringe, P = pelagic, and S = SAV.

Habitat Association	CDFW Bay Study Midwater Trawl	CDFW Fall Midwater Trawl	USFWS Sacramento Midwater Trawl	USFWS Chipps Island Midwater Trawl	CDFW Bay Study Otter Trawl	UCD Suisun Marsh Otter Trawl	CDFW Summer Townet	CDFW 20mm Survey	USFWS Mossdale Kodiak Trawl	CDFW Spring Kodiak Trawl	USFWS Sacramento Kodiak Trawl	USFWS Beach Seine Survey	UCD Suisun Marsh Beach Seines	DWR Yolo Bypass Beach Seine	South Delta Salvage	
B	0.00	0.04	0.05	0.02	0.40	0.10	0.07	0.30	0.20	0.08	0.03	0.42	0.09	0.71	0.35	**Bigscale Logperch**
B	0.03	0.00	0.04	0.02	0.03	0.41	0.00	0.04	0.13	0.00	0.06	0.10	0.04	0.50	0.18	**Black Bullhead**
B	0.23	0.30	0.24	0.13	0.62	0.28	0.36	0.47	0.53	0.07	0.28	0.17	0.07	0.33	0.51	**Channel Catfish**
B	0.11	0.13	0.00	0.07	0.27	0.04	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	**Green Sturgeon***
B	0.13	0.14	0.25	0.20	0.41	0.18	0.05	0.10	0.41	0.25	0.50	0.07	0.00	0.05	0.33	**Pacific Lamprey***
B	0.49	0.34	0.00	0.27	0.96	0.55	0.15	0.30	0.00	0.16	0.00	0.39	0.57	0.13	0.26	**Pacific Staghorn Sculpin***
B	0.09	0.08	0.00	0.13	0.39	0.71	0.09	0.57	0.13	0.09	0.00	0.30	0.45	0.46	0.51	**Prickly Sculpin***
B	0.03	0.05	0.18	0.17	0.05	0.58	0.02	0.32	0.33	0.00	0.13	0.69	0.29	0.38	0.28	**Sacramento Sucker***
B	0.32	0.21	0.00	0.25	0.53	0.64	0.26	0.56	0.20	0.32	0.00	0.27	0.45	0.55	0.28	**Shimofuri Goby**
B	0.00	0.54	0.26	0.22	0.66	0.63	0.57	0.53	0.48	0.23	0.22	0.19	0.24	0.40	0.69	**White Catfish**
B	0.38	0.36	0.00	0.29	0.49	0.29	0.05	0.23	0.00	0.08	0.00	0.00	0.00	0.03	0.24	**White Sturgeon***
B	0.62	0.46	0.05	0.43	0.84	0.78	0.51	0.81	0.15	0.23	0.04	0.46	0.75	0.46	0.63	**Yellowfin Goby**
F	0.07	0.15	0.15	0.17	0.05	0.48	0.14	0.14	0.35	0.20	0.28	0.30	0.23	0.66	0.38	**Black Crappie**
F	0.22	0.29	0.24	0.29	0.26	0.63	0.18	0.31	0.84	0.17	0.26	0.37	0.40	0.61	0.80	**Common Carp**
F	0.03	0.06	0.10	0.09	0.06	0.37	0.11	0.10	0.28	0.00	0.26	0.21	0.17	0.28	0.22	**Goldfish**
F	0.03	0.11	0.08	0.10	0.04	0.27	0.02	0.02	0.09	0.21	0.11	0.35	0.11	0.27	0.14	**Hitch***
F	0.15	0.29	0.26	0.19	0.08	0.50	0.37	0.40	0.95	0.77	0.64	1.00	1.00	1.00	0.51	**Mississippi Silverside**
F	0.03	0.13	0.07	0.15	0.00	0.13	0.00	0.08	0.25	0.07	0.09	0.20	0.12	0.42	0.35	**Sacramento Blackfish***
F	0.09	0.15	0.36	0.28	0.15	0.29	0.02	0.04	0.21	0.37	0.47	0.58	0.32	0.48	0.17	**Sacramento Pikeminnow***
F	0.51	0.40	0.34	0.62	0.50	0.85	0.36	0.38	1.00	0.48	0.22	0.66	0.61	0.57	0.77	**Sacramento Splittail***
F	0.00	0.03	0.07	0.02	0.03	0.00	0.00	0.00	0.20	0.05	0.08	0.23	0.02	0.12	0.00	**Spotted Bass**
F	0.45	0.27	0.02	0.40	0.41	0.77	0.39	0.46	0.00	0.60	0.10	0.34	0.64	0.07	0.21	**Threespine Stickleback***
F	0.15	0.16	0.23	0.32	0.51	0.79	0.14	0.16	0.24	0.15	0.18	0.41	0.53	0.36	0.32	**Tule Perch***
F	0.00	0.02	0.06	0.14	0.00	0.02	0.00	0.00	0.05	0.00	0.21	0.13	0.00	0.36	0.24	**Warmouth**
F	0.00	0.04	0.05	0.11	0.08	0.12	0.08	0.15	0.13	0.13	0.12	0.56	0.39	0.84	0.26	**Western Mosquitofish**
P	0.92	0.86	0.71	1.00	0.55	0.49	0.52	0.48	0.58	0.69	0.44	0.34	0.32	0.31	0.78	**American Shad**
P	0.67	0.45	1.00	0.94	0.35	0.21	0.22	0.29	0.82	0.78	1.00	0.76	0.34	0.72	0.57	**Chinook Salmon***
P	0.60	0.67	0.26	0.74	0.47	0.41	0.72	0.61	0.15	0.82	0.21	0.36	0.29	0.19	0.46	**Delta Smelt***
P	1.00	1.00	0.07	0.86	0.99	0.72	0.59	1.00	0.06	0.65	0.10	0.16	0.20	0.03	0.40	**Longfin Smelt***
P	0.26	0.23	0.44	0.44	0.03	0.09	0.02	0.00	0.30	0.50	0.51	0.34	0.06	0.08	0.35	**Steelhead/Rainbow Trout***
P	0.87	0.91	0.30	0.85	1.00	1.00	1.00	0.88	0.61	0.42	0.16	0.43	0.74	0.48	1.00	**Striped Bass**
P	0.74	0.94	0.57	0.69	0.45	0.58	0.63	0.81	0.89	1.00	0.67	0.73	0.62	0.84	0.95	**Threadfin Shad**
S	0.11	0.20	0.21	0.24	0.14	0.14	0.11	0.17	0.62	0.38	0.39	0.45	0.10	0.74	0.53	**Bluegill**
S	0.04	0.07	0.08	0.09	0.03	0.06	0.04	0.00	0.14	0.04	0.18	0.20	0.05	0.39	0.21	**Green Sunfish**
S	0.07	0.07	0.09	0.18	0.08	0.00	0.12	0.21	0.39	0.20	0.22	0.45	0.06	0.52	0.45	**Largemouth Bass**
S	0.06	0.08	0.15	0.13	0.27	0.04	0.00	0.04	0.45	0.19	0.31	0.43	0.02	0.44	0.25	**Redear Sunfish**

Table 1.3. Mean R values for species assemblages for each of the surveys and SWP salvage by habitat association (Appendix Table 1.2). Conditional formatting applied with darker green representing assemblage representation. Mean R values for each assemblage, across surveys/salvage, presented in right column.

Habitat Association	CDFW Bay Study Midwater Trawl	CDFW Fall Midwater Trawl	USFWS Sacramento Midwater Trawl	USFWS Chipps Island Midwater Trawl	CDFW Bay Study Otter Trawl	UCD Suisun Marsh Otter Trawls	CDFW Summer Townet	CDFW 20mm Survey	USFWS Mossdale Kodiak Trawl	CDFW Spring Kodiak Trawl	USFWS Sacramento Kodiak Trawl	USFWS Beach Seine Survey	UCD Suisun Marsh Beach Seines	DWR Yolo Bypass Beach Seine	South Delta Salvage	Mean R Value
Benthic	0.20	0.22	0.09	0.18	0.47	0.43	0.18	0.35	0.21	0.13	0.10	0.26	0.25	0.33	0.37	**0.25**
Fringe	0.13	0.16	0.16	0.22	0.17	0.40	0.14	0.17	0.35	0.25	0.23	0.41	0.35	0.46	0.34	**0.26**
Pelagic	0.72	0.72	0.48	0.79	0.55	0.50	0.53	0.58	0.49	0.69	0.44	0.45	0.37	0.38	0.64	**0.56**
SAV	0.07	0.11	0.13	0.16	0.13	0.06	0.07	0.10	0.40	0.20	0.27	0.38	0.06	0.53	0.36	**0.20**

Appendix

Appendix Table 1.1. Descriptions of SFE surveys included in analysis. Information sourced from survey metadata (IEP 2018, CDFW 2019).

Long Term SFE Surveys

Survey	Agency	Years of Sampling	Timeframe	Method	Location(s)	Number of Stations	Sampling Intensity	Survey Purpose	Area Sampled
San Francisco Bay Study	CDFW	1980 - Present	Year Round	Midwater Trawl	South Bay, Central Bay, San Pablo Bay, Suisun Bay, West Delta, Lower Sacramento River, Lower San Joaquin River	35 historic, 17 added between 1988-1994	All stations sampled once per month; 12 complete surveys/year.	To determine effects of freshwater outflow on abundance and distribution of fish and mobile crustaceans	Mid - Oblique retrieval
San Francisco Bay Study	CDFW	1980 - Present	Year Round	Otter Trawl	South Bay, Central Bay, San Pablo Bay, Suisun Bay, West Delta, Lower Sacramento River, Lower San Joaquin River	35 historic, 17 added between 1988-1994	All stations sampled once per month; 12 complete surveys/year.	To determine effects of freshwater outflow on abundance and distribution of fish and mobile crustaceans	Bottom
Fall Midwater Trawl	CDFW	1967 - Present (less 1974 and 1979)	September - December	Midwater Trawl	San Pablo Bay, Napa River, Suisun Bay, Delta, Lower Sacramento River, Lower San Joaquin, Deepwater Ship Channel	100 historic, 22 added between 1990-2010	All stations sampled once per month; generally, 9 days to sample all stations. Four complete surveys/year.	Age-0 Striped Bass, Delta Smelt, American Shad, Longfin Smelt, Splittail, and Threadfin Shad Abundance	Mid
Summer Townet	CDFW	1959 - Present	June - August	Tow Net	Napa River, Suisun Bay and Sloughs, Delta, Lower Sacramento River	32 historic, 8 added in 2011 for Delta Smelt	All stations sampled 2-5 times/yr historically, standardized to 6/yr in 2003	Age-0 Striped Bass and Delta Smelt Abundance	Bottom
20mm Survey	CDFW	1995 - Present	April - July	Egg and Larval Tow	San Pablo Bay, Napa River, Suisun Bay, Delta, Lower San Joaquin, Deepwater Ship Channel	54	8-10 complete surveys/year, conducted fortnightly	Postlarval-juvenile Delta Smelt distribution and abundance	Oblique - Bottom, Mid, Surface

Appendix Table 1.1. Continued.

Survey	Agency	Years of Sampling	Timeframe	Method	Location(s)	Number of Stations	Sampling Intensity	Survey Purpose	Area Sampled
Spring Kodiak Trawl	CDFW	2002 - Present	January - May	Kodiak Trawl	Napa River, Suisun Bay, Delta, Lower Sacramento River, Lower San Joaquin River	40	All stations sampled once per month; generally, 4-5 days to sample all stations. Five complete surveys/year.	Abundance and distribution of spawning Delta Smelt	Surface
Beach Seine Survey	USFWS	1976 - Present	Year Round. Three sites on Sacramento River only sampled October - January	50ft Beach Seine	Central Bay, San Pablo Bay, Delta, Lower Sacramento River, Middle Sacramento River, Lower San Joaquin River	58	0.5-3 days per week depending on station. Majority of sites sampled once per week	Juvenile Salmon and other resident fishes monitoring	Beach
Chipps Island Trawl	USFWS	1976 - Present	Year Round	Midwater Trawl	Suisun Bay	1	Three times per week	Juvenile Salmon abundance monitoring	Surface
Mossdale Trawl	USFWS	1994 - Present	Year Round	Kodiak Trawl	Lower San Joaquin River	1	Three times per week	Juvenile Salmon abundance monitoring	Surface
Sacramento Trawl	USFWS	1988 - Present	April - September	Midwater Trawl	Lower Sacramento River	1	2-3 times per week	Juvenile Salmon abundance monitoring	Surface
Sacramento Trawl	USFWS	1994 - Present	October - March	Kodiak Trawl	Lower Sacramento River	1	Three times per week	Juvenile Salmon abundance monitoring	Surface
Suisun Marsh Fish Study	UC Davis	1979 - Present	Year Round	Beach Seine	Suisun Marsh	3	All stations sampled once per month	Resident fish abundance monitoring	Beach
Suisun Marsh Fish Study	UC Davis	1979 - Present	Year Round	Otter Trawl	Suisun Marsh	21	All stations sampled once per month	Resident fish abundance monitoring	Bottom
Yolo Bypass Beach Seine	DWR	1998 - Present	Year Round	Beach Seine	Yolo Bypass - Perenial Pond, Toe Drain, Floodplain	14	Biweekly	Juvenile fish abundance monitoring	Beach

Appendix Table 1.2. List of Delta species included in quantitative species-survey rating analysis.

Habitat associations refer to general areas in which species are found.

Species	Native	Anadromous	Salt Tolerance	Habitat Association
American Shad	N	Y	High	Pelagic
Bigscale Logperch	N	N	Low	Benthic
Black Bullhead	N	N	Med	Benthic
Black Crappie	N	N	Low	Fringe
Bluegill	N	N	Low	SAV
Channel Catfish	N	N	Med	Benthic
Chinook Salmon	Y	Y	High	Pelagic
Common Carp	N	N	Med	Fringe
Delta Smelt	Y	N	Med	Pelagic
Goldfish	N	N	Med	Fringe
Green Sturgeon	Y	Y	High	Benthic
Green Sunfish	N	N	Low	SAV
Hitch	Y	N	Med	Fringe
Largemouth Bass	N	N	Low	SAV
Longfin Smelt	Y	N	High	Pelagic
Mississippi Silverside	N	N	Med	Fringe
Pacific Lamprey	Y	Y	High	Benthic
Pacific Staghorn Sculpin	Y	N	High	Benthic
Prickly Sculpin	Y	N	High	Benthic
Redear Sunfish	N	N	Low	SAV
Sacramento Blackfish	Y	N	Med	Fringe
Sacramento Pikeminnow	Y	N	Med	Fringe
Sacramento Sucker	Y	N	Med	Benthic
Shimofuri Goby	N	N	High	Benthic
Sacramento Splittail	Y	N	Med	Fringe
Spotted Bass	N	N	Low	Fringe
Steelhead/Rainbow Trout	Y	Y	High	Pelagic
Striped Bass	N	Y	High	Pelagic
Threadfin Shad	N	N	Med	Pelagic
Threespine Stickleback	Y	N	High	Fringe
Tule Perch	Y	N	Med	Fringe
Warmouth	N	N	Low	Fringe
Western Mosquitofish	N	N	High	Fringe
White Catfish	N	N	Med	Benthic
White Sturgeon	Y	Y	High	Benthic
Yellowfin Goby	N	N	High	Benthic

Appendix Table 1.3. Species codes and common names for 167 species that have been captured by SFE surveys. Asterix indicates species that have been caught fewer than 10 times since 1959. Species scientific names can be found in Page et al. (2013).

Species Code	Common Name	Species Code	Common Name
AMESHA	American Shad	DELSME	Delta Smelt
ARRGOB	Arrow Goby	DIATUR	Diamond Turbot
BARSUR	Barred Surfperch	DOVSOL	Dover Sole*
BATRAY	Bat Ray	DWAPER	Dwarf Perch
BAYGOB	Bay Goby	ENGSOL	English Sole
BAYPIP	Bay Pipefish	EULACH	Eulachon*
BIGLOG	Bigscale Logperch	FATMIN	Fathead Minnow
BIGSKA	Big Skate	GIAKEL	Giant Kelfish*
BLABUL	Black Bullhead	GOLDFI	Goldfish
BLACRA	Black Crappie	GOLSHI	Golden Shiner
BLAPER	Black Perch	GRESMO	Grey Smoothhound*
BLAROC	Black Rockfish	GRESTU	Green Sturgeon
BLUCAT	Blue Catfish*	GRESUN	Green Sunfish
BLUEGI	Bluegill	HALFMO	Halfmoon*
BLUROC	Blue Rockfish*	HARDHE	Hardhead
BMOSOL	Bigmouth Sole*	HITCH	Hitch
BONSCU	Bonyhead Sculpin	HORTUR	Hornyhead Turbot
BRNTRT	Brown Trout*	JACKSM	Jacksmelt
BROBUL	Brown Bullhead	JACMAC	Jack Mackerel*
BROILO	Brown Irish Lord*	KELGRE	Kelp Greenling
BROROC	Brown Rockfish	KELPER	Kelp Perch*
BROSMO	Brown Smoothhound	LARBAS	Largemouth Bass
BROSSH	Broadnose Sevengill Shark*	LEOSHA	Leopard Shark
BUFSCU	Buffalo Sculpin	LINGCO	Lingcod
BUTSOL	Butter Sole*	LONMUD	Longjaw Mudsucker
CABEZO	Cabezon	LONSME	Longfin Smelt
CALGRU	California Grunion	MISSIL	Mississippi Silverside
CALHAL	California Halibut	MUSBLE	Mussel Blenny*
CALLIZ	California Lizardfish	NIGSME	Night Smelt
CALROA	California Roach	NORANC	Northern Anchovy
CALSKA	California Skate	ONEFRI	Onespot Fringehead
CALSUR	Calico Surfperch	PACBAR	Pacific Barracuda*
CALTON	California Tonguefish	PACBON	Pacific Bonito*
CHACAT	Channel Catfish	PACCMA	Pacific Chub Mackerel*
CHAGOB	Chameleon Goby	PACERA	Pacific Electric Ray
CHEGOB	Cheekspot Goby	PACHAL	Pacific Halibut*
CHISAL	Chinook Salmon	PACHER	Pacific Herring
COHSAL	Coho Salmon*	PACLAM	Pacific Lamprey
COMCAR	Common Carp	PACPOM	Pacific Pompano
COSOLE	C-O Sole*	PACSAN	Pacific Sanddab
CREKEL	Crevice Kelpfish	PACSAR	Pacific Sardine
CURSOL	Curlfin Sole	PACSAU	Pacific Saury*

Appendix Table 1.3. Continued.

Species Code	Common Name	Species Code	Common Name
PACSLA	Pacific Sand Lance	SPEDAC	Speckled Dace*
PACSSC	Pacific Staghorn Sculpin	SPESAN	Speckled Sanddab
PACTOM	Pacific Tomcod	SPIDOG	Spiny Dogfish
PADSCU	Padded Sculpin*	SPLITT	Sacramento Splittail
PENGUN	Penpoint Gunnel	SPOBAS	Spotted Bass
PILPER	Pile Perch	SPOCEE	Spotted Cusk-Eel
PLAMID	Plainfin Midshipman	SPOSUR	Spotfin Surfperch*
PRISCU	Prickly Sculpin	STAFLO	Starry Flounder
PUMPKI	Pumpkinseed	STRBAS	Striped Bass
PYGPOA	Pygmy Poacher	STRKEL	Striped Kelpfish*
QUEENF	Queenfish	STRMUL	Striped Mullet
RAIKIL	Rainwater Killifish	STRSEA	Striped Seaperch*
RAISEA	Rainbow Seaperch*	SURSME	Surf Smelt
RAITRO	Steelhead/Rainbow Trout	THORNB	Thornback
REDBAS	Redeye Bass	THRSHA	Threadfin Shad
REDGUN	Red Gunnel*	THRSHR	Thresher Shark*
REDILO	Red Irish Lord*	THRSTI	Threespine Stickleback
REDSHI	Red Shiner	TIDGOB	Tidewater Goby*
REDSUN	Redear Sunfish	TIDSCU	Tidepool Sculpin
REDSUR	Redtail Surfperch	TOPSME	Topsmelt
RIFSCU	Riffle Sculpin*	TUBESN	Tubesnout*
RIVLAM	River Lamprey	TUICHU	Tui Chub*
ROKSOL	Rock Sole*	TULPER	Tule Perch
RSYSHN	Rosyface Shiner	VERROC	Vermilion Rockfish*
RUBSEA	Rubberlip Seaperch	WAKASA	Wakasagi
SACBLA	Sacramento Blackfish	WALSUR	Walleye Surfperch
SACPER	Sacramento Perch*	WARMOT	Warmouth
SACPIK	Sacramento Pikeminnow	WESBLA	Western Brook Lamprey*
SACSUC	Sacramento Sucker	WESMOS	Western Mosquitofish
SADGUN	Saddleback Gunnel	WHICAT	White Catfish
SADSCU	Saddleback Sculpin*	WHICRA	White Crappie
SANSOL	Sand Sole	WHICRO	White Croaker
SCASCU	Scalyhead Sculpin*	WHISEA	White Seaperch
SHIGOB	Shimofuri Goby	WHISEB	White Seabass
SHIPER	Shiner Perch	WHISME	Whitebait Smelt
SHOGOB	Shokihaze Goby	WHISTU	White Sturgeon
SHOGUI	Shovelnose Guitarfish	WOLEEL	Wolf Eel*
SHOSNA	Showy Snailfish	YELBUL	Yellow Bullhead
SILSUR	Silver Surfperch	YELGOB	Yellowfin Goby
SLISNA	Slipskin Snailfish*	YELROC	Yellowtail Rockfish
SMABAS	Smallmouth Bass	YELSEE	Yellow Snake Eel*
SNAPRI	Snake Prickleback*		

Chapter 2

A Spatiotemporal History of Key San Francisco Estuary Pelagic Fish Species

Dylan K. Stompe[1,2]

Peter B. Moyle[1]

Kiva L. Oken[3]

James A. Hobbs[2]

John R. Durand[1]

Affiliation

[1]*Center for Watershed Sciences, University of California, Davis, 1 Shields Ave, Davis CA 95616*

[2]*California Department of Fish and Wildlife, Region 3, 2825 Cordelia Road #100, Fairfield, CA 94534*

[3]*National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Blvd E., Seattle, WA 98112*

Abstract

Estuaries across the globe have been subject to extensive abiotic and biotic changes and are often monitored to track trends in species abundance. The San Francisco Estuary is a novel ecosystem that has been deeply altered by anthropogenic factors, resulting in fish declines over the past 100 years. To track these species declines, a patchwork of monitoring programs has operated regular fish surveys dating back to the late 1950s. While most of these surveys are designed to track population-scale changes in fish abundance, they are methodologically distinct, with different target species, varying spatial coverage and sample frequency, and differing gear types. To remediate for individual survey limitations, we modeled pelagic fish distributions with integrated data from many sampling programs. We fit binomial generalized linear mixed models with spatial and spatiotemporal random effects to map annual trends in the distribution of detection probabilities of striped bass, Delta smelt, longfin smelt, threadfin shad, and American shad for the years 1980 to 2017. Detection probabilities decreased dramatically for these fishes in the Central and South Delta, especially after the year 2000. In contrast, Suisun Marsh, one of the largest tidal marshes on the west coast of the United States, acted as a refuge habitat with reduced levels of decline or even increased detection probabilities for some species. Our modeling approach demonstrates the power of utilizing disparate datasets to identify regional trends in the distribution of estuarine fishes.

Keywords

Estuary; fish; monitoring; modeling; spatial; spatiotemporal; distribution; San Francisco

Introduction

Estuaries are highly productive and often urbanized systems located at the interface between freshwater and marine environments. Biological productivity is fueled through the input of both terrestrial and marine nutrients, as well as through increased residence time due to salinity-driven density gradients and tidal forcing (Pérez-Ruzafa et al. 2011). Estuaries support diverse assemblages of aquatic species along the salinity gradient, from obligate stenohaline species at the marine and freshwater fringes to oligohaline species that can utilize the entirety of the estuary (Whitfield et al. 2022). The high productivity and location of estuaries at the interface between freshwater and marine environments has also resulted in the general colonization of estuaries by humans seeking the benefit of rich food sources and protected ports (Wilson 1988; Lotze et al. 2006; Cabral et al. 2022).

The dynamic nature of estuaries has encouraged, and in some cases necessitated, environmental modification for human habitation. Many large estuaries have been diked, drained, and dredged for urbanization, transport, water management, flood control and agriculture. Inflows have been diverted or impounded in reservoirs (Cabral et al. 2022). These changes have substantially altered abiotic conditions and have in some cases increased the habitability of estuaries to non-native species (Cabral et al. 2022; Moyle and Stompe 2022.). Species introductions are common in estuaries through ballast water exchange of hitchhiking organisms from international shipping traffic. Recreational, ornamental, and bait species are also often introduced (Moyle and Stompe 2022).

Estuaries are frequently monitored to track trends in the abundance and distribution of aquatic species of recreational, commercial, and cultural importance, many of which have declined because of extensive abiotic and biotic changes (Blaber et al. 2022; Cowley et al. 2022).

Estuarine monitoring is often undertaken by state, federal, tribal, academic, and/or non-governmental organizations, all with potentially different objectives (Anderson 2005). The often-piecemeal implementation of surveys complicates traditional analyses of species trends. In some cases, this results in underutilization of data due to concerns about differences in methodology and bias (Stompe et al. 2020; Huntsman et al. 2022). Unfortunately, logistical and/or financial limitations of surveys means that trends in abundance and distribution of estuarine species are often incomplete when based on analysis of a single survey.

The San Francisco Estuary (Estuary) is a well-monitored system in which data resources have not been fully utilized. The Estuary includes the tidally influenced portions of the Sacramento and San Joaquin Rivers, the Delta, Suisun Bay and Marsh, San Pablo Bay, Central and Southern San Francisco Bay; it terminates at the Golden Gate (Figure 2.1). Habitats within the Estuary are diverse and include pelagic marine habitats, salt, brackish, and freshwater marshes, low gradient riverine habitats, and freshwater littoral habitats, among others.

The Estuary has been highly altered by myriad abiotic and biotic changes since large-scale colonization by European-Americans in the 1800s. Abiotic changes include extensive physical and hydrologic alterations in the form of water diversions, levees, floodplain and marshland reclamation, construction of dams on every major river in the Estuary's 163,000 km^2 watershed, and the severe disruption of natural sedimentation regimes due to historic hydraulic mining and the current impoundment of sediment behind dams (Cloern and Jassby 2012; Whipple et al. 2012; Schoellhamer et al. 2013; Herbold et al. 2014). Sometimes called the most heavily invaded estuary in the world, the Estuary has also been subject to numerous species invasions through ballast water dumping in its freshwater and saltwater ports, and state-sponsored and illicit intentional introductions (Cohen and Carlton 1998). As a result of these changes, and other stressors such as overfishing (Yoshiyama et al. 1998) and pollution (Brooks et al. 2012), many native and some introduced fish species have experienced drastic declines in the past 100 years, and especially the last 40 years (Sommer et al. 2007; Stompe et al. 2020).

Along with numerous smaller diversions, the Estuary contains two major water export facilities located in the South Delta, the State Water Project (SWP) and Central Valley Project (CVP; Figure 2.1), which export a large proportion of freshwater inflow for agricultural and municipal use (Gartrell et al. 2017; Moyle et al. 2018). To track the impacts of these water infrastructure operations on Estuary fish species, state and federal agencies and a research group at the University of California, Davis (UC Davis), have operated regular fish surveys dating back to the late 1950s (Honey et al. 2004; Herrgesell 2012; Tempel et al. 2021). Early surveys primarily focused on tracking the abundance of young of year striped bass, an introduced yet recreationally and culturally important species within the Estuary (Turner and Chadwick 1972; Chadwick et al. 1977; Stevens et al. 1985). Later, additional surveys were started to track the abundance and survival of outmigrating juvenile salmonids (Dekar et al. 2013) and to track changes in fish and invertebrate assemblages (Baxter et al. 1999; O’Rear et al. 2021) rather than single species.

While most Estuary fish surveys are designed to track fish abundance over a wide spatial expanse, they are logistically and economically restricted in total number of stations and frequency of sampling events. In addition, surveys sample different micro- and macro-habitats due to differences in gear type, spatial coverage, and project goals (Tempel et al. 2021). Since fish species are not homogenous in their distribution throughout the water column or Estuary, differences in catch arise because of these disparities (Stompe et al. 2020).

In this paper, we leverage an integrated dataset of eight long-term Estuary surveys (Stompe et al. 2020) to examine trends in the distribution and abundance of several important fish species. Species included are striped bass (*Morone saxatilis*), Delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), threadfin shad (*Dorosoma petenense*), and American shad (*Alosa sapidissima*). We use spatially-explicit species distribution modeling to fit binomial generalized linear mixed models to the integrated survey data and then 1) identify key areas of importance for these species over time, 2) pinpoint time periods of major shifts in distribution and abundance, and 3) describe the effects of freshwater outflow on distribution.

Methods

Study Species

The species selected for our analysis (striped bass, Delta smelt, longfin smelt, threadfin shad, American shad) were chosen due to their ecological, cultural, and recreational significance in the Estuary. These species represent important recreational fisheries (striped bass and American shad) and both native (Delta smelt, longfin smelt) and introduced (threadfin shad) forage fishes. In addition, all these fishes require productive estuarine pelagic environments during part or all their lives (Moyle 2002), so their abundances can be indicators of the 'health' of pelagic habitats.

Striped bass is an introduced, relatively long-lived, semi-anadromous, and fecund species that relies on productive estuaries for rearing (Raney 1952). Since their introduction, they have been one of the primary catch species in agency and university surveys, although catches have declined considerably over the years (Kohlhorst 1999; Sommer et al. 2007).

Delta smelt is a small native osmerid endemic to the Estuary. They are generally an annual species and are an obligate estuarine species (Moyle et al. 1992; Moyle 2002). Despite once high abundance, they are now rarely caught by Estuary surveys and are listed as threatened under the Federal Endangered Species Act (FESA) and endangered under the California Endangered Species Act (CESA; Tempel et al. 2021).

Like Delta smelt, longfin smelt are small native osmerids; they are found along the Pacific Coast of North America, are more halophilic than Delta smelt, and can live two to three years (Moyle 2002). Historically, they were highly abundant within the Estuary but have since declined and are now relatively rare (Sommer et al. 2007). As a result, they were listed as threatened under the CESA in 2009 (Tempel et al. 2021).

Threadfin shad are introduced, small, deep bodied clupeids that typically live two to three years (Moyle 2002). Despite their somewhat recent introduction to the system, threadfin shad have also experienced declines in abundance (Sommer et al. 2007).

American shad are another introduced clupeid species, but they reach larger sizes than threadfin shad and generally migrate into the Pacific Ocean after rearing in the Estuary (Moyle 2002). Unlike the above-described fishes, previous work has not identified major reductions in Estuary American shad abundance and instead has seen recent increases in angler catch (Ferguson 2016).

Survey Data

The surveys included in our modeling effort are the California Department of Fish and Wildlife (CDFW) Fall Midwater Trawl (FMWT; White 2021), CDFW Bay Study Otter and

Midwater Trawls (BSOT, BSMT; Baxter et al. 1999), CDFW Summer Townet Survey (STN; Malinich 2020), UC Davis Suisun Marsh Otter Trawl and Beach Seine Surveys (SMOT, SMBS; O'Rear et al. 2021), United States Fish and Wildlife Service (USFWS) Beach Seine Survey (BSS; McKenzie 2021a), and the USFWS Chipps Island Trawl (CIT; McKenzie 2021b; Table 2.1). Of the stations we include in our analysis, there is considerable spatial overlap between the surveys in the San Pablo, Carquinez, Suisun, and Sacramento-San Joaquin Confluence Regions (Figure 2.1 – Regions 3-6; Appendix Figure 2.1). Conversely, the Bay Study Otter Trawl and Bay Study Midwater Trawl are the only surveys with stations in the Central and South San Francisco Bays (Figure 2.1 – Regions 1 and 2; Appendix Figure 2.1) and only the Fall Midwater Trawl, Summer Townet Survey, Beach Seine Survey, and Chipps Island Trawl have stations in the Delta (Figure 2.1 – Regions 7-9; Appendix Figure 2.1). The longest running of these surveys (Summer Townet Survey) started in 1959 and the most recent (Bay Study Otter and Midwater Trawls) in 1980, and all have operated continuously on at least an annual basis through 2017. Several of these surveys were originally designed to describe and track trends in young of year striped bass abundance (Fall Midwater Trawl, Summer Townet Survey), some were designed to track the outmigration of juvenile salmonids through the Estuary (Chipps Island Trawl, Beach Seine Survey), and others were designed to track assemblages of fish and invertebrate populations (Suisun Marsh Otter Trawl/Beach Seine, Bay Study Otter and Midwater Trawls). All were implemented to determine the effects of water diversion and/or entrainment into export facilities on fish populations. These surveys primarily capture small and/or juvenile fishes due to their specific gear types and netting mesh sizes. For this reason, surveys are generally able to describe trends in the relative abundance of small fishes such as Delta smelt, Longfin smelt, and threadfin shad, but only represent juvenile trends for large fishes, such as striped bass and American shad.

Data from these surveys were integrated into an aggregate dataset for the years 1980 through 2017, retaining key variables such as date, coordinates, and number of individual fish captured by species (Stompe et al. 2020). For consistency of annual spatial extent, we only include those survey stations which were sampled at least once annually in our analyses. In addition, several Beach Seine Survey stations located on the Sacramento River upstream of the Delta were omitted because of their distance from other downstream stations. Because effort shifted among certain years, data used from the Chipps Island Trawl was seasonally restricted to April through June and from the Fall Midwater Trawl to September through December to standardize seasonal effort. All other surveys generally operated year-round.

Catch per unit effort was calculated as total number of fish caught per seine or trawl, with a total of 103,341 sampling events. While other Estuary data integration efforts have instead chosen to index catch by the volume of water sampled (Huntsman et al. 2022), not all surveys we include record this metric, nor is it as meaningful of a metric for some gear types (i.e. beach seines). In addition to indexing catch per trawl or seine, we included species presence or absence for each sample. The inclusion of a binary metric allows for the modeling of probability of detection, regardless of water volume sampled.

In this integrated format, these data represent approximately 40 years of trends in Estuary fish abundance at a much greater seasonal and spatial density than could be provided by any single survey. In addition, the breadth of gear types included in the eight-survey dataset mean that benthic, pelagic, and littoral species are all targeted to some degree.

Data Analysis

Using the aggregate eight-survey dataset, we modeled spatiotemporal trends in the probability of detection of the previously described fish species using the package 'sdmTMB' (Anderson et al. 2022). We constructed and fit binomial generalized linear mixed models (GLMMs) of species presence by maximum likelihood for each of the five fish species from the aggregate dataset across a restricted spatial mesh. Model predictions from the binomial models represent the probability of detection rather than the total predicted catch of a given species. Because of this, these models do not necessarily capture absolute changes in abundance. However, binomial model predictions do provide some index of changes in abundance because survey gear is more likely to detect species at higher densities assuming they are relatively evenly distributed within the sampled habitats and assuming limited density dependence of catch (Godø et al. 1999). During model construction Tweedie distributions (Tweedie 1984) were also tested, but model fit was poor with this distributional family (Hartig 2022).

A spatial mesh for efficiently modeling spatial and spatiotemporal autocorrelation was generated using the "cutoff" method, with a minimum of 2km spacing between mesh vertices ("knots") and resulting in a mesh with 179 knots (Anderson et al. 2019). Knot spacing was iteratively chosen to reduce model overfitting in highly sampled areas of the Estuary (Suisun Bay, Carquinez, etc.), while also providing acceptable spatial coverage in less intensively sampled areas.

The spatial mesh was geographically restricted to the wetted area of the Estuary by restricting spatial autocorrelation between geographically close, yet ecologically distinct, habitats (Figure 2.1). Shorelines were simplified using barrier polygons, and small channels were expanded to allow the mesh to fit an adequate number of knots for even representation of sparsely sampled areas. Likewise, only major islands separating heterogeneous habitats were included to increase the number of knots in the sinuous regions of the Delta and Suisun Marsh. Finally, the Montezuma Slough Salinity Control Gates and Delta Cross Channel Gates were treated as open to reflect the average condition during sampling periods (Figure 2.1). Simplification of the barrier polygon was an iterative process, as early barrier polygons with full shoreline and channel complexity had very few knots present in the Delta and Suisun Marsh regions.

The notational structure (Equation 1) of the binomial GLMMs is shown below. The number of sampling events that detected a given species at location *s* in year *t* and month *m* by sampling program p, $y_{s,t,m,p}$ is modeled as a binomial random variable with expected probability of detection at a single sampling event equal to $\mu_{s,t,m,p}$ and $N_{s,t,m,p}$ sampling events over the month. We used a logit link to model $\mu_{s,t,m,p}$ as a function of independent year effects (α_t), survey effects (β_p), and a cubic spline for month (*s(m)*). The variable ω_s represents spatial random effects, $\epsilon_{s,t}$ represents spatiotemporal random effects, and ζ_t represents the spatially varying coefficients through time Y (scaled year *t* centered around zero with a standard deviation equal to one). The random effects (ω_s, $\epsilon_{s,t}$) and the spatially varying coefficient (ζ_t) are drawn from Gaussian Markov random fields with Matérn covariance matrices Σ_ω, Σ_ϵ, and Σ_ζ, respectively (Barnett et al. 2021). Spatial random effects were included to account for unmeasured variables that are approximately fixed through time (depth, distance upstream, substrate, etc.) whereas spatiotemporal random effects were included to account for unmeasured variables that are likely to change over both time and space (salinity, temperature, food availability, etc.; Anderson et al. 2022). Spatiotemporal random effects were treated as independent and identically distributed.

$$y_{s,t,m,p} \sim Binomial\left(N_{s,t,m,p}, \mu_{s,t,m,p}\right),$$

$$logit\left(\mu_{s,t,m,p}\right) = \alpha_t + \beta_p + s(m) + \omega_s + \epsilon_{s,t} + \zeta_t Y_t$$

$$\omega_s \sim MVNormal(0, \Sigma_\omega)$$

$$\epsilon_{s,t} \sim MVNormal(0, \Sigma_\epsilon)$$

$$\zeta_t \sim MVNormal\left(0, \Sigma_\zeta\right)$$

Equation 1

Residuals from the non-random effects were then simulated by drawing 500 samples from the fitted model and tested using the 'DHARMa' package in R (Hartig 2022). Residual uniformity was tested using the one-sample Kolmogorov-Smirnov test, residual dispersion was tested using the DHARMa nonparametric dispersion test via the standard deviation of residuals fitted versus simulated, and residual outliers were tested using the DHARMa outlier test based on the exact binomial test with approximate expectations (Hartig 2022). None of the models demonstrated unacceptable levels of residual uniformity, dispersion, or outliers, indicating good fit.

Previous publications have identified the potential pitfalls of generating models using disparate datasets in an integrated format (Walker et al. 2017; Moriarty et al. 2020; Huntsman et al. 2022). When unaccounted for, differences in survey effort, gear efficiency, and overall catchability can introduce significant biases in abundance and spatiotemporal density trends (Walker et al. 2017; Huntsman et al. 2022). However, our inclusion of survey as a fixed effect accounts for these biases, allowing separate intercepts to be fit for each of the eight surveys.

Once models were fit, predictions of the probability of detection and spatially explicit slopes of predictions over time were made for each of the five species across a 500m grid of the wetted area for the visualization of Estuary wide trends. Estimates of the spatial slope standard deviation as a metric of uncertainty were then generated by sampling (n=200) from the joint precision matrix.

Once prediction dataframes were made, the mean estimates of the probability of detection were calculated by decade for each spatial point and means were rasterized into smooth prediction planes using the R package 'ggplot2' (Wickham 2016). Rasterized spatial slopes, representing relative change through time, were plotted along with the standard deviation of the estimates of the spatial slopes. Mean annual estimates of the probability of detection at grid points for each of the five species were also plotted by applying a smoothing function (generalized additive model) by year.

To measure distributional sensitivity to changes in Delta outflow conditions (amount of water exiting the Delta after water exports) and overall shifts in population distributions, we calculated the annual predicted center of gravity (COG) and 95% confidence intervals along a longitudinal gradient for each of the modeled fish species. Delta outflow data was sourced from the California Department of Water Resources (CDWR 2022) as millions of acre-feet of water per calendar year. COG is a metric which represents the mean location of a population, weighted by density of observations, and although it is imperfect at describing local trends and/or detecting changes at distributional extremes (Barnett et al. 2021), it can be a useful metric for measuring population movement along a distributional gradient (Thorson et al. 2016). Due to computational limitations, COG estimates were generated using predictions at survey station points rather than at all points on the prediction grid. As a result, the COG of each species does not necessarily represent the true longitudinal center of each population, but changes in COG over time and relative differences between species are valid. COG was calculated longitudinally to best reflect the flow direction of the Estuary, which generally runs East-West from the Delta through the Central San Francisco Bay (Figure 2.1).

To test for the effects of Delta outflow on COG, temporal trends in COG, and differences in COG between species, we constructed a generalized additive model using the package "mgcv" (Pseudo-R Code, Equation 2; Wood 2011). The point estimates of COG for each species from the sdmTMB prediction outputs were included as the response variable, with yearly estimates weighted by their variance. Smooth functions with thin plate basis splines (bs="tp") were applied to "Year" by "Species" and "Delta Outflow" by "Species", and "Species" was included as a linear fixed effect. Finally, generalized additive model results were printed in tabular format and plots were generated of yearly COG point estimates, 95% confidence intervals around the point estimates, the fit trendline and 95% confidence interval by species from the generalized additive model, and the spline effect of Delta outflow in million-acre feet on COG (Wickham 2016; Coretta 2022).

$$COG \sim s(Year, by = Species, bs = "tp") + s(Delta\ Outflow, by = Species, bs = "tp") + Species$$
$$weights = variance$$

Equation 2

All analyses were conducted in R version 4.1.2 (R Core Team 2020). Code is available on github (https://github.com/dkstompe/SFE_Spatial_Fishes.git).

Results

Model Results

All models fully converged and fit the data acceptably well as determined through residual testing in the DHARMa package (Hartig 2022). The results of residual dispersion tests and residual outlier tests were significant for some models (Appendix Table 2.1); however, this was driven by the exceptionally large number of data points included in the model rather than poor model fit (Hartig 2022). For example, the dispersion value of 0.992 for the American shad model was significant (p=0.012) as was the outlier test (p=0.0083) with just 467 outliers out of 103,341 observations. The results of model diagnostics are included in the supplementary material (Appendix Figure 2.2, Appendix Table 2.1).

The output of the GLMMs showed differing coefficients by 'Survey' for all species as well as negative coefficients for the linear component of the smooth effect of 'Month' sampled for threadfin shad and American shad (Table 2.2). The differing coefficients by 'Survey' indicate differences in the catchability of species by survey methodology and gear type, while the negative coefficient of the linear component of 'Month' is likely due to seasonal differences in either local abundance, absolute abundance, or vulnerability of capture across life stages for the two shad species.

As expected, the pelagic gear types used by surveys such as the Bay Study Midwater Trawl, the Fall Midwater Trawl, and the Chipps Island Trawl were generally most effective at catching the pelagic species included in our analysis as indicated by model coefficients, with some notable exceptions (Table 2.2). For example, the Fall Midwater Trawl, a survey specifically designed to capture young of year striped bass, had a lower model coefficient than the reference survey (Bay Study Midwater Trawl). Beach seines and benthic trawls typically had negative coefficients amongst the modeled fish species, indicating lower capture efficiencies than the reference survey (Bay Study Midwater Trawl).

Spatial Trends

In general, species show an overall reduction in spatial probabilities of detection over the modeled time period (Figure 2.2). Spatial slopes are negative in most regions for most species and are exclusively negative or near zero for Delta smelt and longfin smelt (Figure 2.3). Positive slope values are present in limited regions for striped bass (Suisun Marsh, North Delta, South San Francisco Bay), threadfin shad (Confluence, Suisun Bay, Suisun Marsh), and American shad (North Delta, Suisun Bay, Suisun Marsh, South San Francisco Bay).

Species show some shared patterns in distributional changes in the probability of detection over time; most notable of which is the reduction in estimates in the Central and South Delta (Figure 2.1 – regions 8-9; Figure 2.2). This trend exists for striped bass, threadfin shad, and American shad which historically had relatively high probabilities of detection in these regions, but which had very low detection probabilities by the 2010s. Further supporting this are the spatial slopes which are strongly negative in the Central and South Delta for these species (Figure 2.3). The reduction in detection probability in these regions drives a constriction in distribution away from large parts of the Delta and towards the Confluence and Suisun regions (Figure 2.1 – region 6 and 5).

Unlike the other three species, the two smelt species were rarely detected in the Central and South Delta regions at any point during the modeled time period. Longfin smelt were mostly distributed downstream, with historically high probabilities of detection in the Central San

Francisco Bay through the Confluence region (Figure 2.1 - regions 2-5). Conversely, Delta smelt were not found in the lower portions of the Estuary and were instead most likely to be detected in the North Delta, Confluence, and Suisun Regions (Figure 2.1 – regions 5-7). Both species seem to exhibit a reduction in overall detection probabilities rather than a constriction of distribution.

Another notable trend is the persistently higher probability of detection in the Suisun Marsh and Suisun Bay regions (Figure 2.1 – region 5 top and bottom, respectively) relative to other parts of the Estuary for all species. For most species it appears that the probability of detection does not increase in Suisun over the decades, but rather it decreases less. This is supported by the spatial slope plots which show relatively less negative slope in the Suisun Bay and especially Suisun Marsh regions (Figure 2.3). American shad was the one species which did have positive slopes throughout much of the Suisun Marsh region, indicating an increased detection probability between 1980 and 2017.

In general, there was little uncertainty in the spatial slopes in highly sampled regions where species were detected by the eight surveys over the modeled time period. Uncertainty was high at the edge of the spatial mesh, such as the north end of San Pablo Bay (Figure 2.1 – region 3), or where species were never or rarely detected (Delta Smelt, Central and South San Francisco Bays, Figure 2.2 & 2.3). Spatial slopes should be interpreted cautiously in these specific areas given the relatively high level of uncertainty.

Detection Trends

The overall probability of detection for the included species generally declined between 1980 and 2017 (Figure 2.4), evidence that abundance may be declining. Declines are most evident for striped bass and the two smelt species, the latter of which are now rarely detected in the eight surveys. Conversely, the detection probabilities for striped bass, threadfin shad, and American shad appear to somewhat rebound near 2017 after lows in 2010 through 2012.

The trends in detection probability are primarily nonlinear, with intermittent periods of increase or stabilization. Striped bass have the largest overall decline, from a detection probability of approximately 0.35 in the early 1980s to less than 0.15 by 2012 (Figure 2.4). Delta smelt have an initial steep decline in the early 1980s, followed by relatively stable to increasing detection probability until another period of steep decline in the early 2000s. After this decline Delta smelt again stabilize until the mid-2010s, at which point they decline to near zero. Longfin smelt trends are similar to Delta smelt, but with a less dramatic initial decline followed by a low in the early 1990s and a rebound in the late 1990s before ultimately declining to near zero as well. Threadfin shad trends are somewhat similar to longfin smelt, but as stated earlier, they have partially recovered in the years since 2010. Finally, American shad are unique in their trends, with a somewhat stable detection probability until a decline in the late 2000s, followed by a recovery after 2010.

Center of Gravity

The generalized additive model (Equation 2) of the smooth effects of year and Delta outflow by species on COG, and of the linear effects of species on COG, fit with an adjusted R squared of 0.969 and explained 97.7% of the deviance in the data.

The center of gravity (COG) of each fish species partitioned by easting, with threadfin shad distributed the furthest upstream (Table 2.3, Figure 2.5). This is followed by Delta smelt, American shad, and striped bass clustered within approximately 5km of one another, and longfin smelt the furthest downstream (Table 2.3, Figure 2.5).

The smooth term for Delta outflow indicated effects of Delta outflow on COG for longfin smelt ($p=1.63e-6$), Delta smelt ($p=6.92e-7$), and threadfin shad ($p<2e-16$), while little to no effect was seen for striped bass ($p=0.069$) or American shad ($p=0.123$; Table 2.4). While effects clearly existed for Delta smelt, longfin smelt, and threadfin shad, the magnitude and direction of shifts in COG at different Delta outflow values were not uniform amongst the species (Figure 2.5). Longfin smelt were the most affected by changes in outflow conditions, with a somewhat linear relationship and an estimated center of gravity more than 15km downstream at high Delta outflow than at the lowest outflow values (Figure 2.5). Delta smelt COG also declined somewhat linearly as Delta outflow increased, although at a lower magnitude than for longfin smelt (Figure 2.5). Changes in threadfin shad COG shifted considerably under different outflow conditions; however, this relationship was non-linear with minima at both 23 and 60+ maf (Figure 2.5).

The point estimates and modeled fit of COG by species also resulted in several distinct patterns over the modeled time period. The smooth term for year indicated effects on COG (Table 2.4) for longfin smelt ($p<2e-16$) and threadfin shad ($p<2e-16$), little effect for Delta smelt ($p<0.071$), and no effect for American shad ($p=0.132$) or striped bass ($p=0.477$). Longfin smelt had the most dramatic temporal trends in COG, spanning approximately 20km over the modeled time period (Figure 2.5). In addition, longfin smelt COGs remained further downstream during the period after 2002, despite some periods of extreme drought (CDEC 2022). Threadfin shad also showed strong temporal trends in COG, but with a unique pattern where the population generally shifted upstream during the period from approximately 1990 through 2010 (Figure

2.5). Finally, Delta smelt remained relatively centered within a 5km band, with little interannual variability (Figure 2.5).

Discussion

Using new developments in spatiotemporal modeling, we leveraged the rich but fragmented monitoring data in the Estuary to demonstrate changes in the spatial and temporal probability of detecting key pelagic fish species during a period of considerable abiotic and biotic change. Large swaths of the Estuary that historically supported high detection probabilities of striped bass, threadfin shad, and American shad, including the South and Central Delta, are now relatively devoid of these species, driving population constrictions to the Suisun and Confluence regions. Over the same time period, Delta smelt and longfin smelt experienced relatively even declines throughout the Estuary. The detection probability of all species declined to some extent from their levels in 1980; however, the trends and future outlooks differ by species.

It is important to note that differences in life history and age-structured distribution of the species can color interpretation. Striped bass is a long-lived semi-anadromous species most likely to be caught by survey gear during their first year of life; results reflect juvenile distribution and are not directly indicative of adult behavior or abundance. Likewise, American shad typically migrate out of the Estuary (and into the Pacific Ocean) after their first year (Carothers et al. 2021), so juveniles are best represented in our results. Longfin smelt also sometimes leave the Estuary; however, they are susceptible to survey gear throughout their lives so results may be interpreted as representing the total local population. Finally, Delta smelt and threadfin shad primarily remain within the Estuary and are vulnerable to survey gear throughout their short (1-3) year lifespans. Specifically, Delta smelt is an annual species (Moyle 2002) fully restricted to the sampled estuarine areas so our results may be interpreted as representing the spatiotemporal trends of the species as a whole.

Given these species-specific differences in model interpretation, it is clear that Delta smelt and longfin smelt have declined precipitously since the 1980s (Figure 2.4). These species are now rarely detected by Estuary surveys. The threadfin shad population has also experienced declines in overall abundance; however, it appears to be more robust in its ability to shift to different regions as evidenced by positive spatial slopes in the Confluence and Suisun regions (Figure 2.3). As a result, threadfin shad overall probability of detection has somewhat recovered since 2010 (Figure 2.4). The most dramatic decline in detection probability is seen for striped bass (Figure 2.4), indicating a reduction in either spawning success or juvenile survival over the modeled time period. American shad spawning success or juvenile survival has also somewhat declined between 1980 and 2017, although their probability of detection is now only slightly below historic highs after a recovery since 2010 (Figure 2.4). The lower level of overall decline in juvenile American shad versus juvenile striped bass, despite similar distributional patterns, may be somewhat driven by increased utilization of Suisun Marsh by American shad as the Central and South Delta became inhospitable (Figure 2.3).

Sensitivity of annual COGs to outflow conditions indicate different relative effects of climate and water management for each of the species. Delta outflow has major effects on the location of the salinity gradient, and thus the highly productive low-salinity zone (MacWilliams et al. 2015). Given that longfin smelt COGs are associated with Delta Outflow (Table 2.4, Figure 2.5), this indicates that the distribution of this species may annually shift to track areas of favorable salinity and/or productivity. Conversely, species such as American shad whose COGs are insensitive to different outflow conditions (Table 2.4, Figure 2.5) may not be as plastic in their annual distribution, potentially due to reliance on habitat structure rather than water conditions. It is difficult to identify whether longitudinal plasticity in response to changes in Delta outflow is advantageous, as both species with highly variable COGs, such as longfin smelt, and species with relatively stable COGs, such as striped bass, have both experienced dramatic declines in their probability of detection.

Trends in annual COG over time suggest differential responses to changing environmental conditions and highlight life history differences among the species (Table 2.3, Figure 2.5). The highly variable annual COGs for longfin smelt and threadfin shad support a plastic response in distribution, or potentially differences in success between multiple subpopulations within the Estuary. For example, multiple spawning populations of longfin smelt have been identified within the Estuary (Lewis et al. 2019), so regional differences in spawning success or survival could shift annual COGs. Conversely, the relatively fixed annual COGs for Delta smelt, striped bass, and American shad indicate a general reliance on fixed habitat features and either no subpopulation structure or subpopulations with similar interannual spawning success or survival.

The abiotic and biotic drivers of the described changes in abundance and distribution are likely complex and interacting. For example, over the modeled time period, the Estuary saw changes in water export regimes (Gartrell et al. 2017), the introduction of several highly invasive plant and invertebrate species (Cohen and Carlton 1998), and both record-setting droughts (Durand et al. 2020) and extremely wet years (CDEC 2021). These factors interact, changing the amount and quality of habitat for native and introduced pelagic fishes.

For example, invasive plants such as Brazilian waterweed (*Egeria densa*) have benefitted from reduced turbidity due to upstream impoundments and the constant freshwater condition maintained by water export operations (Durand et al. 2016). Dense stands of Brazilian waterweed have reduced water velocity in some areas, dropping out additional suspended particulate matter and capturing nutrients from upstream sources (Yarrow et al. 2009; Durand et al. 2016). This has resulted in potentially reduced pelagic productivity (Vanderstukken et al. 2011; Durand et al. 2016), a shift in zooplankton communities important for small and larval fish diets (Espinosa-Rodríguez et al. 2021), and reduced turbidity, which makes small fishes more susceptible to predation (Ferrari et al. 2014). There are myriad examples of such interacting and cascading effects that have reduced the suitability of the pelagic habitat within the Estuary (Brown and Moyle 2005; Sommer et al. 2007; Brooks et al. 2012; Cloern and Jassby 2012; Sabal et al. 2016).

An overarching trend in the distribution and regional abundance of these species is the relative insulation of the Suisun Region, and to a lesser degree the North Delta, from overall declines in detection probability (Figure 2.2, 2.3). There are many potential drivers of this, one of which is likely the historically lower levels of colonization of submersed aquatic vegetation, such as Brazilian Waterweed, in these regions. Brazilian waterweed is largely limited by salinity in Suisun Marsh and Bay (Borgnis and Boyer 2016) and was previously limited by turbidity in the North Delta (Durand et al. 2016). Given their relatively lower levels of decline in detection probability, these regions could prove important for maintaining viable populations of pelagic fishes in the future.

Despite lower levels of decline or even increased detection probability in the Suisun region and the North Delta, it should be noted that these regions may not necessarily represent *ideal* habitat in the face of system wide degradation. These regions may simply be *better* than those regions which have experienced substantial declines in detection probability (Central Delta, South Delta). Under this scenario, fish may be shunted away from previously productive habitats into regions which have experienced relatively less change. This likely partially explains the increased detection probability of some species in Suisun Bay and Marsh and the North Delta over the modeled time period.

It should be noted that the station density is somewhat sparse in the North and South Delta, with one or few surveys representing catch in these regions. Specifically, trends in the North Delta are most influenced by catch from the USFWS Beach Seine Survey, while trends in the south Delta are most influenced by catch from the Summer Townet Survey (Appendix Figure 2.1). These regional differences in station density and representation should be considered when interpretating the absolute detection probability of species such as Delta smelt in the North Delta.

Conclusions

By leveraging existing long-term survey data in an integrated modeling format, we have described trends in the distribution and abundance of five key Estuary fish species. The modeling techniques we employ have most commonly been used to describe trends in large adult marine fishes, but we demonstrate their ability to model trends in juvenile or small estuarine fishes as well. Our approach also demonstrates the value of using an integrated data set due to the greatly increased spatial density and coverage. These data can detect distributional trends that would otherwise not be covered by a single survey. We are aware that measures must be taken to ensure that modeling with disparate data does not impart unacceptable biases, so we included ‘survey’ as a fixed effect and only used consistently surveyed stations. These should be sufficient to control for the methodological disparities. Our modeling and data integration methods should not only prove useful for management of Estuary fishes, but also for describing trends in distribution and abundance of fishes in other inland, estuarine, and marine systems with multiple independent surveys.

The individual long-term fish surveys of the Estuary have collected valuable data for tracking trends in the distribution and abundance of the species we considered here, and indeed for most fish species found within the Estuary. While any one survey can describe part of a species' story, it is only when surveys are analyzed in concert that we can see the true extent of change. The increased spatial breadth and detail of an integrated analysis allows us to see much more granular and localized changes in distribution.

The Estuary has experienced dramatic changes to its hydrology, biotic communities, and physical structure, which in turn has reduced the detection probability and distributional breadth of both native and naturalized pelagic fish species. The species analyzed here include fish that hold considerable ecological, recreational, and cultural value amongst California stakeholders. We show, through distributional shifts and spatial slopes, that a major driver in the reduced detection probability of pelagic fishes is the declines in their populations in large portions of the Delta. Conversely, Suisun Marsh and the North Delta appear to function as refuge habitats for at least a few of the species, reinforcing that they should be managed as high priority refuges for conservation.

While our analyses identify regions and time periods of change for these fish species, they do not specifically identify biological or abiotic drivers of these changes. In future efforts, our models may be expanded through the inclusion of spatially explicit data for both biotic and abiotic predictors, including bathymetry, temperature, and LIDAR imagery of submersed aquatic vegetation. Expansion of our models in this way would further refine our understanding of important habitat criteria for pelagic fishes in the Estuary, which should result in more effective habitat restoration and conservation.

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Figures

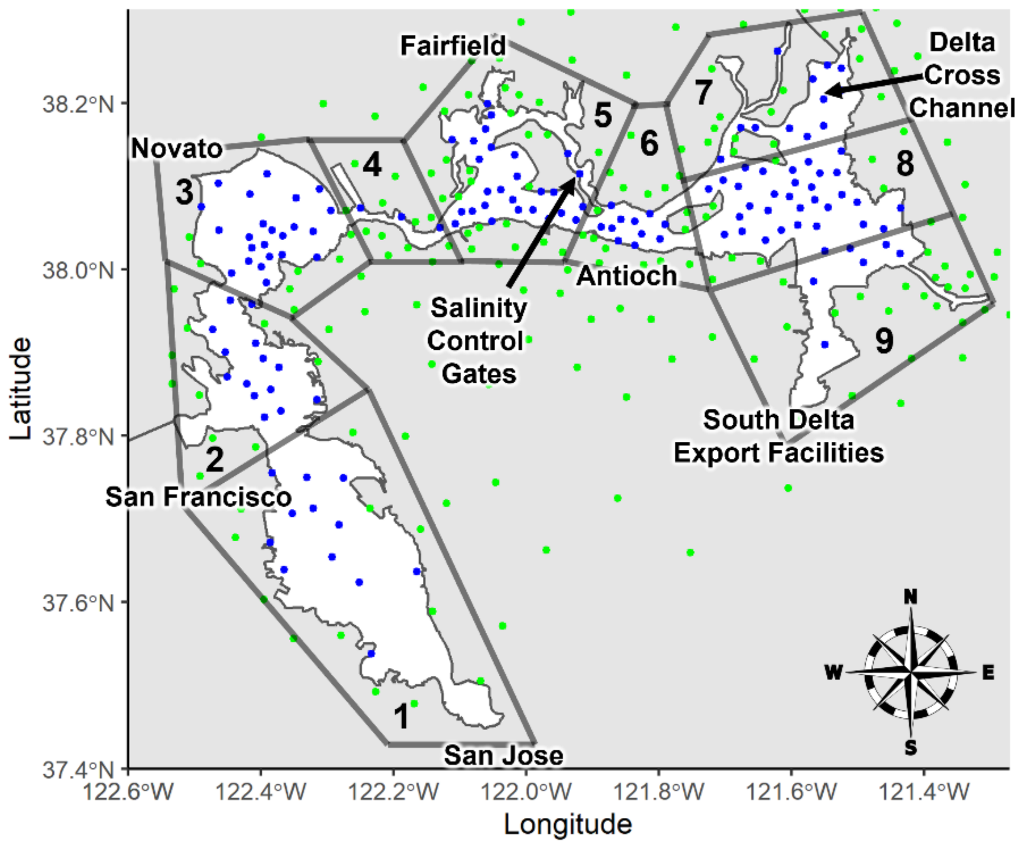


Figure 2.1. Simplified spatial plane of the San Francisco Estuary with applied barrier components. White background is wetted area and grey background is land. Blue dots represent the center of "water" spatial mesh triangles and green dots represent the center of "land" spatial mesh triangles. Select cities surrounding the Estuary, the location of the Montezuma Slough salinity control gates, the location of the Delta Cross Channel, and the location of the South Delta export facilities (State Water Project, Central Valley Project) are included for reference. Numbered regions are identified for regional descriptions of distribution trends. 1 = South San Francisco Bay, 2 = Central San Francisco Bay, 3 = San Pablo Bay, 4 = Carquinez Strait, 5 = Suisun Marsh (top) and Suisun Bay (bottom), 6 = Sacramento-San Joaquin Confluence, 7 = North Delta, 8 = Central Delta, 9 = South Delta.

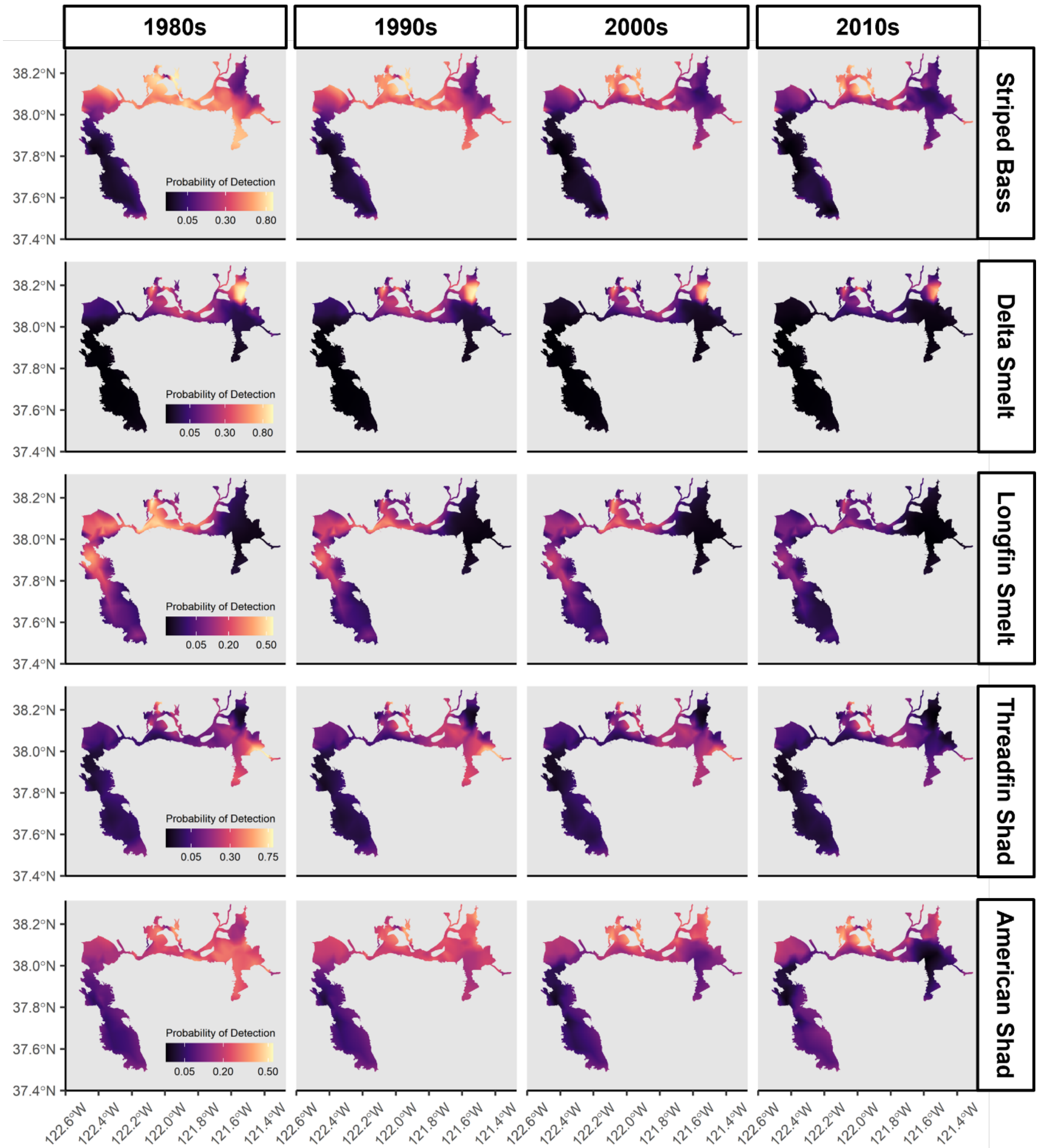


Figure 2.2. Mean probability of distribution of striped bass, Delta smelt, longfin smelt, threadfin shad, and American shad by decade, as predicted by GLMMs. Hotter colors denote higher probability of detection, cooler colors lower probability of detection. Note: color scales are on a square root scale.

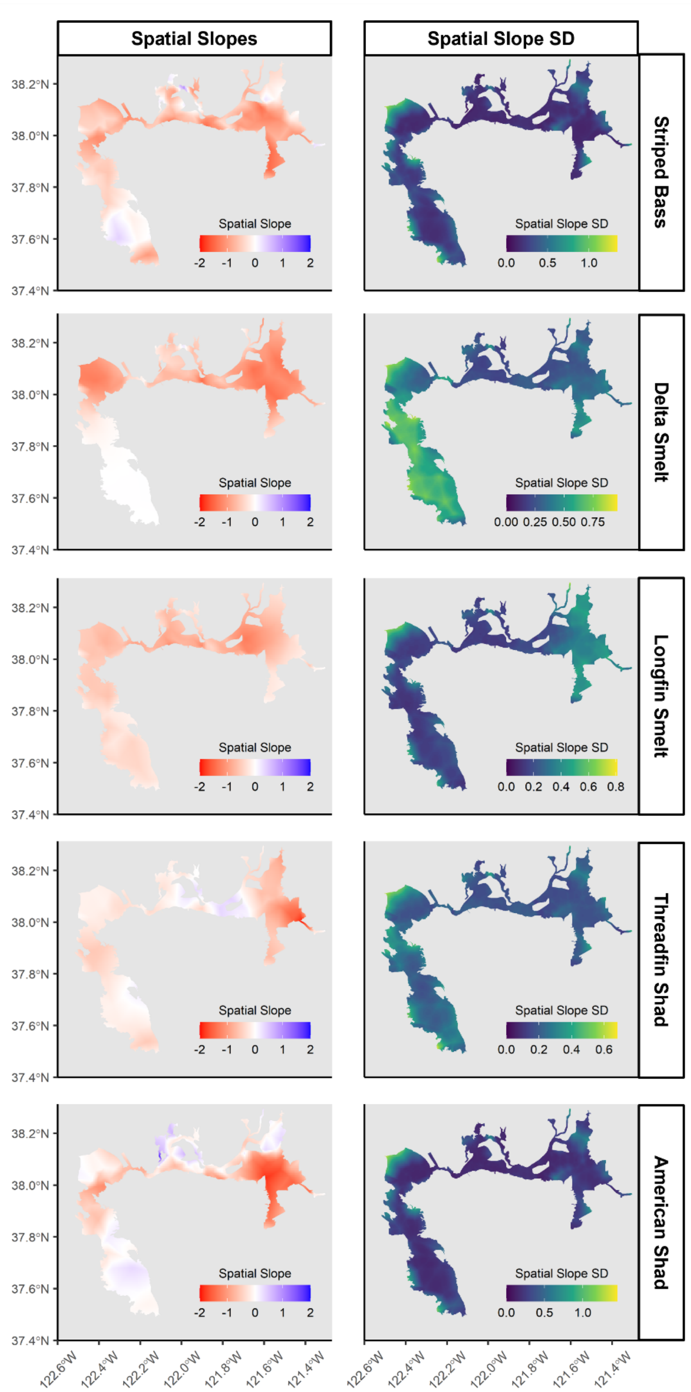


Figure 2.3. Spatial slopes and standard deviations (SD) of spatial slopes for the five modeled fish species. Red slope shading indicates a decrease in the probability of detection between 1980 and 2017, white is no change, and blue indicates increased probability of detection. Hotter colors indicate higher SD and thus increased uncertainty in model predictions of spatial slope.

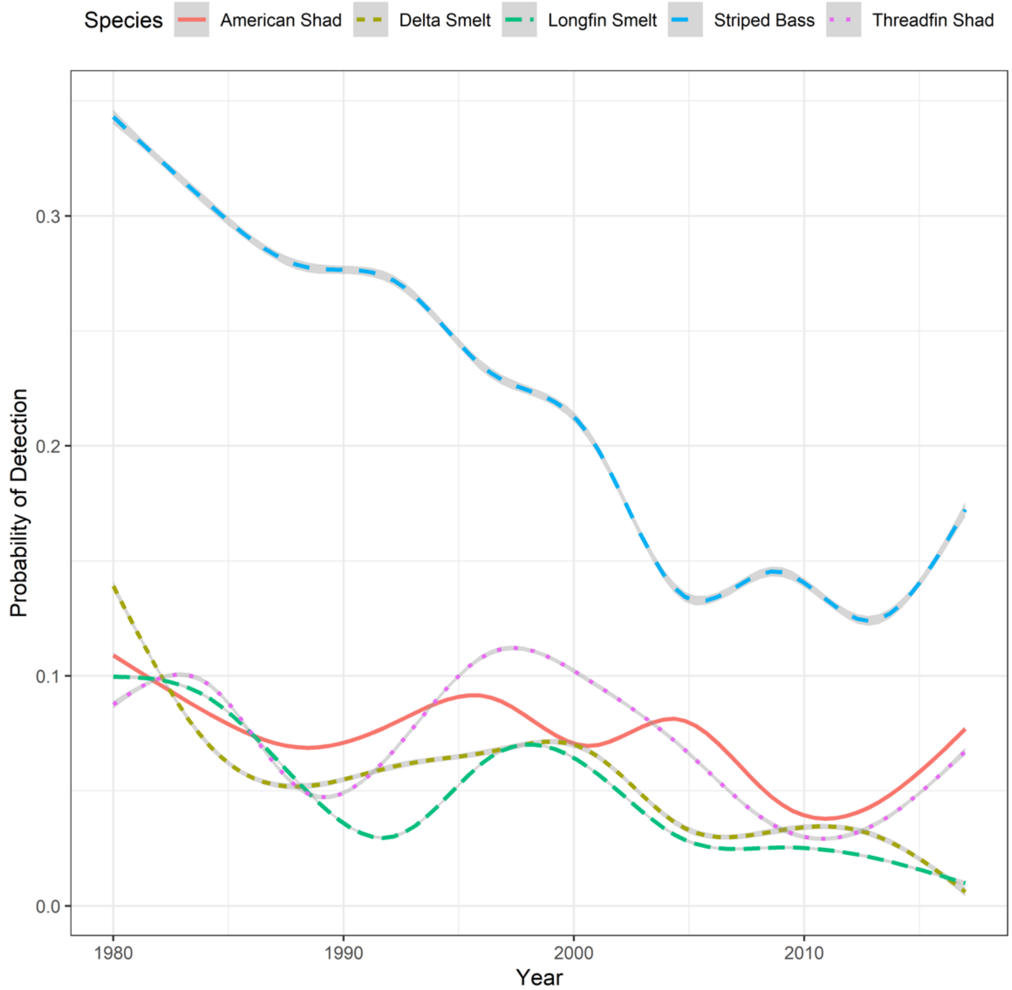


Figure 2.4. Overall trends in the predicted probability of detection by the eight-survey aggregate dataset as calculated by generalized additive model smoother of estimates at 500m grid points.

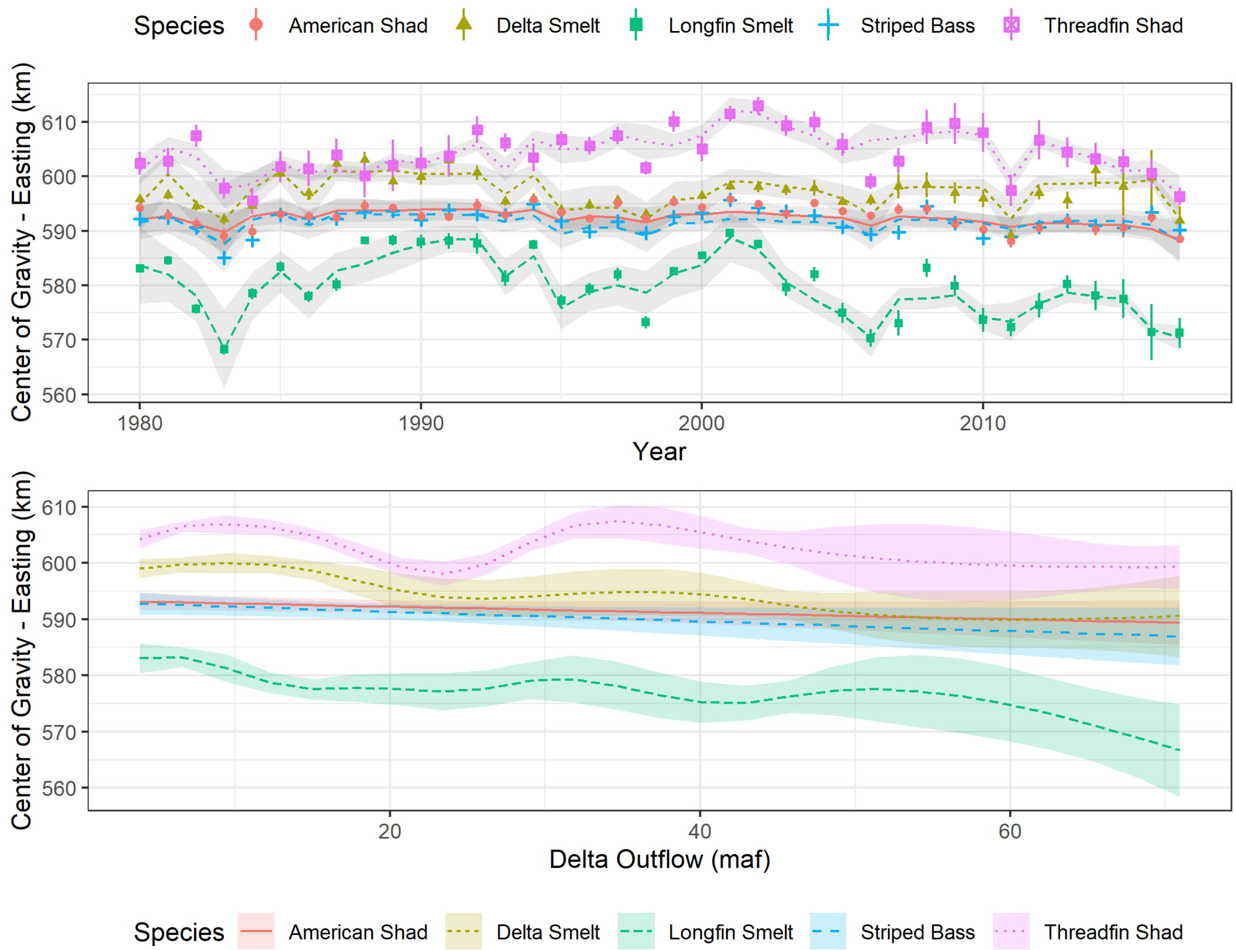


Figure 2.5. Top panel is the center of gravity (COG) of the five modeled fish species from 1980-2017, shown as yearly point estimates with 95% confidence intervals as well as via generalized additive model fit (Equation 2). Bottom panel are the estimated smooths of the center of gravity for each species across values of Delta outflow, measured in million-acre feet (maf).

Tables

Table 2.1. Surveys, number of stations, and total number of samples included in eight-survey dataset. Samples are indexed as individual trawl or seine pulls. CDFW = California Department of Fish and Wildlife and USFWS = United States Fish and Wildlife Service.

Agency	Survey	Number of Stations	Samples
CDFW	Fall Midwater Trawl	88	15,934
CDFW	Bay Study Otter Trawl	33	13,790
CDFW	Bay Study Midwater Trawl	32	12,904
CDFW	Summer Tow Net	31	13,842
UC Davis	Suisun Marsh Fish Otter Trawl	17	7,782
USFWS	Beach Seine Survey	14	14,002
USFWS	Chipps Island Midwater Trawl	1	23,700
UC Davis	Suisun Marsh Beach Seine	1	1,387

Table 2.2. Model results from binomial generalized linear mixed models of probability of detection for striped bass, Delta smelt, longfin smelt, threadfin shad, and American shad. Table contains factor (Survey) and smooth (Month) model coefficients and standard errors. The Intercept term is assigned to the CDFW Bay Study Midwater Trawl. Matérn range is the distance at which spatial correlation degrades to ~0.13. Survey abbreviations are as follows: BOT = CDFW Bay Study Otter Trawl, BSS = USFWS Beach Seine Survey, CIT = USFWS Chipps Island Trawl, FMWT = CDFW Fall Midwater Trawl, SMBS = UC Davis Suisun Marsh Beach Seine, SMOT = UC Davis Suisun Marsh Otter Trawl, STN = CDFW Summer Townet Survey.

	Striped Bass		**Delta Smelt**		**Longfin Smelt**		**Threadfin Shad**		**American Shad**	
	coef.est	**coef.se**	**coef.est**	**coef.se**	**coef.est**	**coef.se**	**coef.est**	**coef.se**	**coef.est**	**coef.se**
(Intercept)	0.79	0.41	-4.89	0.92	-4.16	0.51	-1.72	0.82	-1.68	0.29
Survey:BOT	-0.09	0.04	-1.41	0.08	0.29	0.03	-1.77	0.1	-2.56	0.07
Survey:BSS	-2.70	0.09	-2.50	0.15	-3.8	0.29	-0.27	0.1	-3.32	0.12
Survey:CIT	-0.40	0.07	0.96	0.10	-0.84	0.08	0.63	0.13	2.51	0.09
Survey:FMWT	-0.29	0.04	0.14	0.07	0.16	0.05	0.27	0.07	0.14	0.05
Survey:SMBS	-1.20	0.17	-1.76	0.44	-1.95	0.32	-0.52	0.25	-3.01	0.27
Survey:SMOT	-0.08	0.12	-2.31	0.26	-0.34	0.16	-1.86	0.19	-2.95	0.17
Survey:STN	-0.61	0.05	0.87	0.08	-0.54	0.06	-0.69	0.1	-1.67	0.07
s(Month)	-0.04	0.00	0.00	0.01	-0.01	0	-0.19	0.01	-0.26	0.01
Matern Range	29.69		29.20		27.30		36.52		24.47	

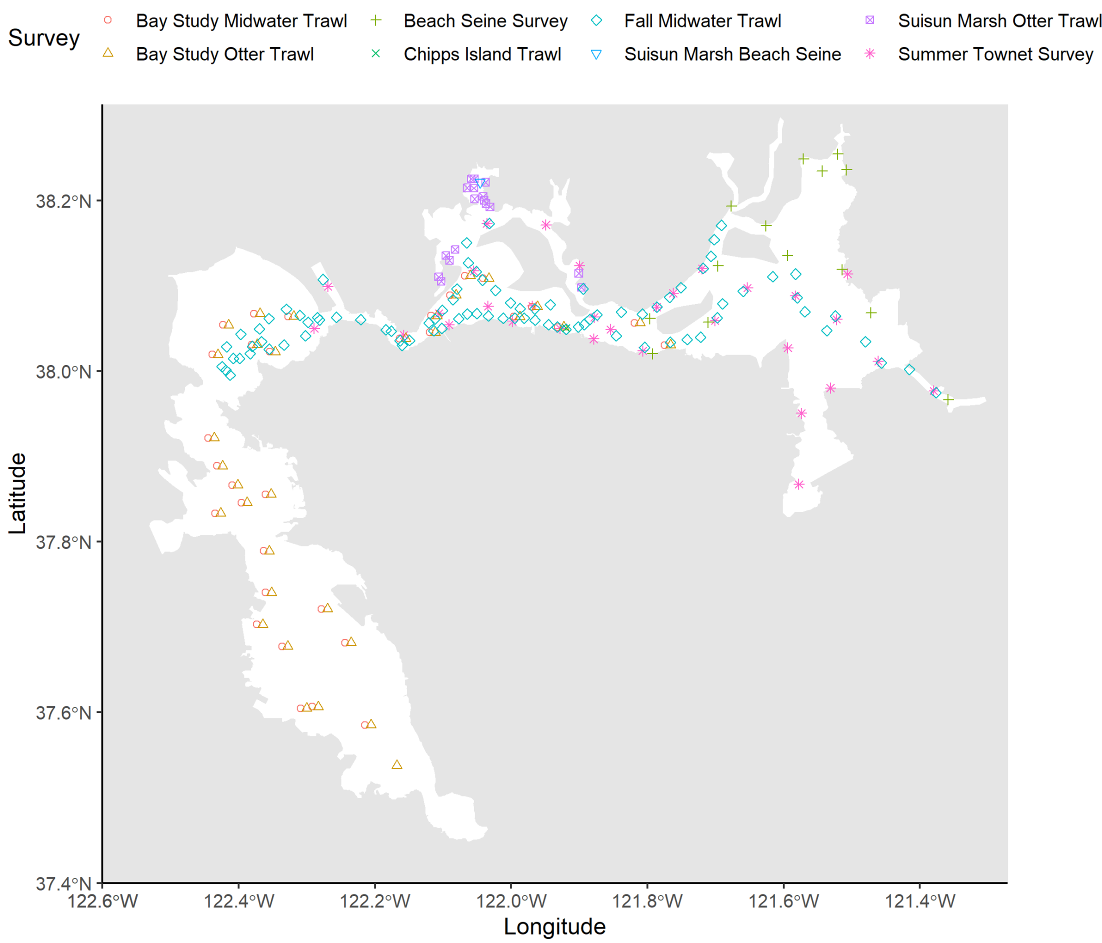
Table 2.3. Model results for the parametric linear terms of COG generalized additive model. Intercept represented by American shad.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	592.3	0.59	1007.2	<2e-16
Delta Smelt	5.0	0.80	6.2	5.45e-9
Longfin Smelt	-12.7	0.75	-16.8	<2e-16
Striped Bass	-0.9	0.93	-0.9	0.357
Threadfin Shad	12.1	0.64	18.8	<2e-16

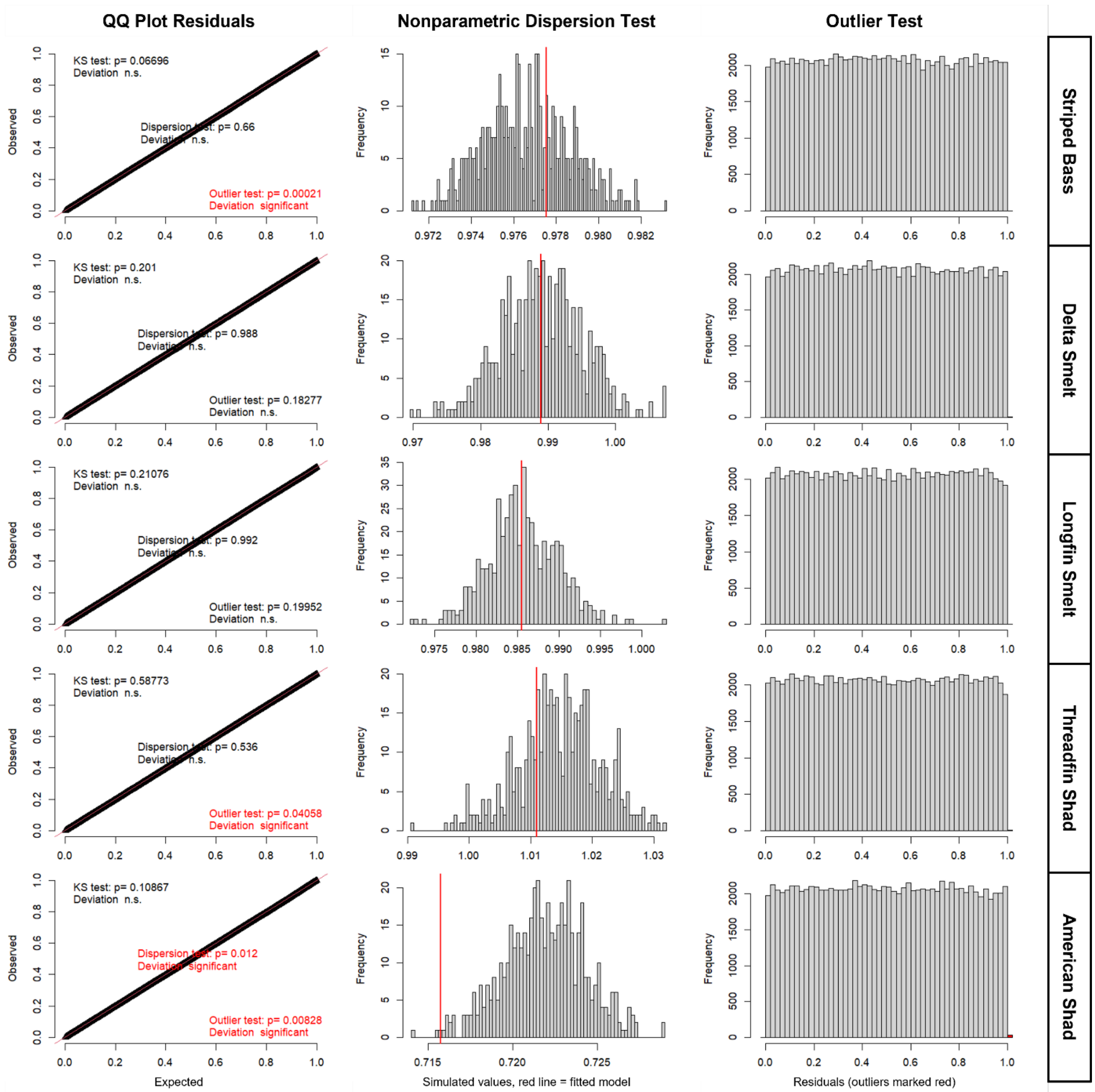
Table 2.4. Model results for the smooth interaction terms from the COG generalized additive model.

	edf	Ref.df	F	p-value
s(Year):American Shad	1.78	2.21	1.99	0.132
s(Year):Delta Smelt	2.87	3.49	2.40	0.071
s(Year):Longfin Smelt	8.50	8.90	13.59	<2e-16
s(Year):Striped Bass	1.00	1.00	0.51	0.477
s(Year):Threadfin Shad	8.60	8.94	13.14	<2e-16
s(Delta Outflow):American Shad	1.00	1.00	2.41	0.123
s(Delta Outflow):Delta Smelt	5.09	5.98	7.73	6.92e-7
s(Delta Outflow):Longfin Smelt	6.88	7.83	6.01	1.63e-6
s(Delta Outflow):Striped Bass	1.00	1.00	3.37	0.069
s(Delta Outflow):Threadfin Shad	7.67	8.48	9.26	<2e-16

Appendix



Appendix Figure 2.1. Location of sampling stations included in generalized linear mixed models of species occurrence. Different colors/shapes represent the eight surveys.



Appendix Figure 2.2. Model diagnostics from DHARMa of fixed effect residuals from binomial GLMMs. Left column is QQ plots of observed versus expected values, middle column is standard deviation of fitted versus simulated residuals, and right column is residual values with outliers marked in red. Uniformity was tested using One-Sample Kolmogorov-Smirnov test, dispersion using DHARMa nonparametric dispersion test via standard deviation of residuals fitted versus simulated, and outliers using DHARMa outlier test based on exact binomial test with approximate expectations.

Appendix Table 2.1. Results of DHARMa (Hartig 2022) testing of fixed effect residual uniformity, dispersion, and outliers. Uniformity was tested using One-Sample Kolmogorov-Smirnov test, dispersion using DHARMa nonparametric dispersion test via standard deviation of residuals fitted versus simulated, and outliers using DHARMa outlier test based on exact binomial test with approximate expectations. Disp. = dispersion value and Num = number of outliers detected at both margins. Significant test results at <0.05 level indicated by *. Significant test results do not necessarily indicate misspecification or poor model fit due to the exceptionally large number of data points. See main text for explanation.

	Uniformity		**Dispersion**		**Outliers**	
	D	**p-value**	**Disp.**	**p-value**	**Num**	**p-value**
Striped Bass	0.0041	0.0670	1.0010	0.6600	339	0.0002*
Delta Smelt	0.0033	0.2010	0.9999	0.9880	385	0.1828
Longfin Smelt	0.0033	0.2108	0.9998	0.9920	386	0.1995
Threadfin Shad	0.0024	0.5877	0.9964	0.5360	371	0.0406*
American Shad	0.0038	0.1087	0.9915	0.0120*	467	0.0083*

Chapter 3

Evidence for Continued Success and Recruitment of Striped Bass (*Morone saxatilis*) in the Umpqua Estuary, Oregon.

Dylan K. Stompe[1,2]

Malte Willmes[3]

Peter B. Moyle[1]

James A. Hobbs[2]

Andrew L. Rypel[1,4]

Levi Lewis[4]

John R. Durand[1]

Affiliation

[1]*Center for Watershed Sciences, University of California, Davis, 1 Shields Ave, Davis CA 95616*

[2]*California Department of Fish and Wildlife, Region 3, 2825 Cordelia Road #100, Fairfield, CA 94534*

[3]*University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA 95064*

[4]*Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 1 Shields Ave, Davis, CA 95616*

Abstract

Given amenable environmental conditions, introduced species often colonize other nearby habitats. This is the case for Striped Bass (*Morone saxatilis*), a relatively long-lived, mobile, and physiologically tolerant species that was introduced to the San Francisco Estuary, California, in 1879 from its native range on the Atlantic Coast of North America. After its introduction, Striped Bass quickly colonized estuaries in southern Oregon, including the Umpqua River Estuary. Despite the persistence of a fishery for Striped Bass in the Umpqua River Estuary, infrequent detections of juveniles brought into question whether this population of Striped Bass was supported by local production or immigration from the larger San Francisco Estuary population. To test this, we prepared and analyzed 23 otoliths from Striped Bass collected by a local angler using laser ablation plasma mass spectrometry. Strontium isotope ratios were measured along a transverse section of otolith and annular rings were overlaid on these data to determine age-specific measurements. Strontium isotope ratios were then converted to salinity estimates based off a salinity mixing model calibrated with local water sample values. Our analyses showed no evidence of immigration from the San Francisco Estuary, with all individuals likely rearing in either the Smith or Umpqua River, or in the brackish portions of the Umpqua River Estuary. Few incidences of movement into high salinity waters were observed, with most individuals remaining in the low salinity portions of the estuary throughout their lives. We also demonstrate a higher spawning frequency than has been seen in the past with the presence of six-year classes within a ten-year period. Overall, the Umpqua Estuary Striped Bass population appears to be restricted to a narrow distributional band and is both self-sustaining and not supported by immigration.

Introduction

The colonization of new areas by introduced species is a common phenomenon (Elton 1958), especially for generalist and physiologically tolerant species (Marchetti et al. 2004, García-Berthou 2007). Species with abilities to tolerate a wide range of conditions and disperse through continuous habitats, such as the marine environment, are likely to be especially good colonizers (Nagelkerken et al. 2015) and may develop metapopulation structure. Metapopulations consist of multiple connected populations (Harrison and Taylor 1997), potentially facilitating invasion as new populations develop along dispersal corridors. The degree to which introduced species develop and rely upon metapopulation dynamics is largely unknown, however, the specific dynamics of introduced metapopulations are likely to change as habitats are altered within individual populations due to development and climate change (Thomas and Hanski 2004).

Striped Bass (*Morone saxatilis*) were introduced into the San Francisco Estuary, California in 1879 as part of a state-sponsored campaign to establish new commercial and recreational fisheries (Smith 1895) and may have subsequently developed metapopulation structure within its non-native range. Striped Bass are a relatively long-lived and large-bodied, anadromous, fecund species native to the Atlantic and Gulf Coasts of the United States (Raney 1952). Their introduction to the San Francisco Estuary quickly resulted in a highly productive fishery in the San Francisco Estuary (Craig 1930), and within six months individuals were captured in the Pacific Ocean (Monterey Bay; Scofield 1931). Striped Bass were detected in Coos Bay, Oregon, starting as early as 1914 (Morgan and Gerlach 1950), and in the following decades, Striped Bass also colonized other ecosystems along the southern Oregon Coast (Parks 1978); this was an unsurprising feat given the highly migratory nature of Striped Bass in their native range (Atlantic Coast; Merriman 1941, Chapoton and Sykes 1961). Establishment of Southern Oregon Striped Bass populations was almost certainly the result of coastal movements from the San Francisco Estuary because no fish were stocked in these ecosystems during this time period (Raney 1952).

Much as in the San Francisco Estuary, Striped Bass populations quickly expanded within Southern Oregon estuaries. Striped Bass were present in high enough numbers to support a commercial fishery by the mid-1920s in the Coos Bay system (Waldman et al. 1998) and by the 1940s in the estuaries of the Smith and Umpqua Rivers (Winchester Bay; Parks 1978). The Coos Bay population of Striped Bass has since mostly disappeared (Waldman et al. 1998, M. Gray pers. comm.), but a small, productive recreational fishery still exists in the Umpqua and Smith Rivers (T. Jarmain pers. comm.; ODFW 2022).

Movement of Striped Bass from the San Francisco Estuary to Southern Oregon estuaries has been demonstrated by the natural establishment of these populations; however, the periodicity of such events is unclear. Whereas extensive coastal migrations by Striped Bass are an annual occurrence on the Atlantic Coast (Clark 1968), coastal movements are far less predictable in the Pacific (Boughton 2020), potentially due to differences in ocean temperatures which may elicit movement (Radovich 1963, Bennett and Howard 1997). As a result, colonization events of Pacific Coast estuaries by Striped Bass from the San Francisco Estuary have been sporadic, as evidenced by low genetic diversity amongst Oregon Striped Bass populations (Waldman et al. 1998).

Local production of Striped Bass in Oregon estuaries is also likely limited. Despite their high physiological tolerance of a range of conditions as adults, Striped Bass require relatively specific environmental conditions for successful spawning (Raney 1952). They are generally supported by intermittently strong year classes generated during years of favorable conditions (Setzler 1980). A 1972 survey of juvenile fishes in the Umpqua Estuary detected young-of-year and age-one Striped Bass (Mullen 1977) which was evidence of local spawning success and recruitment in this Southern Oregon system. Conversely, extensive monthly sampling over a later, ten-year period (1977-1986) did not detect any juvenile Striped Bass in the Umpqua Estuary, despite a local recreational fishery for adults during the same time period (Johnson et al. 1986). Taken together, both serve as evidence that spawning was inconsistent at best and the Oregon population was likely reliant on rare spawning events and/or on immigration from other systems.

Anecdotal reports suggest an increasingly productive fishery in the Umpqua Estuary (ODFW 2022), as well increased catch of smaller Striped Bass (T. Jarmain pers. comm). Yet it remains unclear whether this population is supported by local production, immigration from the San Francisco Estuary or other Southern Oregon estuaries, or a combination of the two. To determine origin and movement history of Striped Bass in the Umpqua Estuary, and thus the potential for metapopulation dynamics, we analyzed strontium isotope ratios within otoliths from Umpqua River Estuary angler-caught Striped Bass. We then use these ratios to determine likely natal watershed and movement history in relation to salinity over the life of each individual. We also investigated estuarine conditions at time-of-spawning in an effort identify potential drivers in local recruitment and to predict potential for changes in recruitment and overall abundance, given climate change. Our study identifies local dynamics of a small, yet persistent, introduced population of an estuarine predator.

Methods

Study Area

The Umpqua River Estuary is a small- to medium-sized estuarine system with two primary freshwater inputs, the Smith and Umpqua Rivers (Figure 3.1). The Smith River enters the Estuary at river kilometer 18.5, drains an area of 899 km^2, and extends 145 km upstream from where it meets the Umpqua (Ratti 1979, Palmer 2014). The Umpqua River is substantially larger, draining an area of 12,103 km^2 extending approximately 179 km from its mouth to the confluence of the North and South Umpqua Rivers (Wallick et al. 2011). Tidal influence extends approximately 43.5 km upstream on the Umpqua River and 38.6 km on the Smith River, resulting in an estuary of approximately 27.6 km^2 (Ratti 1979).

Water Samples

Water samples were collected for chemical analysis at eight sites in the Umpqua River, ten sites in the Smith River, six sites in the Umpqua Estuary, three sites in the Coos Bay Estuary, and two sites in the Coquille River Estuary (Figure 3.1). Coquille and Coos Bay sites were included as nearby outgroups to the Umpqua Estuary since these systems are geographically close and either currently support (Coquille River) or historically supported (Coos Bay) populations of Striped Bass. In the Umpqua River, Smith River, and Umpqua Estuary, water samples were collected along a salinity gradient from totally fresh (0 ppt salinity) to fully marine (30.9 ppt) as measured with a calibrated YSI Pro 2030 handheld meter. Water was collected at fully marine stations in Coos Bay (29-33.1 ppt) and at brackish (16.7 ppt) to fully marine (33.2 ppt) stations in the Coquille River Estuary. In addition to salinity, time of day, conductivity, dissolved oxygen (percent and mg/L), water temperature, Secchi depth, and tidal state were recorded at each site when possible.

Water samples were analyzed for Strontium isotope ratios and total Strontium concentrations by the University of California Davis (UCD) Interdisciplinary Center for Plasma Mass Spectrometry. Strontium 87/86 ratios were reported and a two-endmember salinity mixing model was generated using the R package 'OGFLtools' (Denny et al. 2022) and the methods outlined in Hobbs et al. (2019). Uncertainty was calculated around the mixing model salinity estimates based on instrumentation standard error of Sr87/Sr86 ratio estimates.

Otolith Collection

Otoliths were collected and donated by a retired local fishing guide who captured Striped Bass in 2019 in the Smith and Umpqua Rivers, Oregon, within the tidal portion of the Umpqua River Estuary (Figure 3.1). Otoliths were collected incidental to legal sportfishing activity. Total length, general location, and date of capture were recorded, and Striped Bass heads were shipped to UCD for otolith extraction and processing. Sex was not recorded. In total, otoliths from 23 Striped Bass were recovered and analyzed.

Otolith Sample Preparation

Sagittal otoliths were prepared at the UCD Otolith Geochemistry & Fish Ecology Laboratory using methods outlined in Willmes et al. (2021). Otoliths were set in silicone molds with Epoxicure (Buehler Scientific) epoxy resin, allowed to sit until fully set (~24hrs), and were adhered to glass microscope slides using thermoplastic resin (Crystalbond 509, Ted Pella Inc. Redding, CA). Otoliths were sectioned through the core region with an Isomet diamond cutting saw after visually identifying the core by projecting light through the slide and marking the core with a fine felt tip marker. Sectioned core regions were mounted on slides using thermoplastic resin and sanded on both sides using 600 to 1200 grit sandpaper until the core was visible under a compound microscope. Once the core had been reached, sections were polished using 0.3 μm MicroPolish II Alumina (Buehler Scientific) on a polishing cloth (Secor et al. 1992, Wells et al. 2003). Otoliths were imaged using AM Scope software, a 12-megapixel digital camera, and a CH30 Olympus compound microscope at 40 times magnification. Once imaged, 23 otoliths were mounted on petrographic glass slides for laser ablation, with nine individual otoliths per slide.

Otolith Laser Ablation

Once prepared, otoliths were brought to the UCD Interdisciplinary Center for Plasma Mass Spectrometry (ICPMS) for laser ablation using a Nd:YAG 213 nm laser (New Wave Research UP213) coupled to a Nu Plasma high resolution multi-collector inductively coupled plasma mass spectrometer (NU032) to measure Strontium 87/Strontium 86 (87Sr/86Sr) isotopic ratios. The laser diameter was set at 40 μm and ran through the core from dorsal to ventral edge at 10 μm/s. Laser pulse rate was set at 10-Hz frequency and 5-15 J/cm^2 photon output. Accuracy of the laser ablation high resolution multi-collector inductively coupled plasma mass spectrometer was tested by ablating a modern marine reference material collected offshore of Baja California (White Seabass otolith) prior to analyzing Striped Bass otoliths. The otolith reference material yielded an 87Sr/86Sr value of 0.70916 ± 0.00008 (n=20, ±2σ) - similar to the global average of modern seawater (0.70918; McArthur et al. 2001, Mokadem et al. 2015).

Otolith Aging

Dark bands, representing the low growth period during winter months (Campana and Thorrold 2001), were identified on otolith cross sections to generate age estimates. Ages from otoliths were first estimated independently by two readers, and any disagreements were resolved by the inclusion of a third reader. Ages were considered final after at least two reads were in agreement. Once ages were finalized, physical distances between annular bands were measured along laser ablation burn lines using a reference scale at 40x (Figure 3.2).

Otolith Data Analysis

Otolith microchemistry data were analyzed in the R package 'IsoFishR' following methods outlined in Willmes et al. (2018). One value per second of laser run time was generated from the raw 87Sr/86Sr mass spectrometer values by averaging point values, and outliers were removed if beyond 2 times the interquartile range within a 40-point moving average window. A smoother was then applied to Otolith 87Sr/86Sr profiles using thin-plate regression splines (k=80) using the MGCV package in R (Wood 2017). Confidence intervals around the smooth spline were calculated from the propagated uncertainty of the reference material.

Ages were assigned to Otolith 87Sr/86Sr profiles based on burn distances between annular bands. 87Sr/86Sr profiles were then standardized so that growth years received an equal distance between annular band. Interannual distances can vary based on age, growth rate, and environmental condition, therefore, standard profiles allow for better comparison of movement patterns between individuals. 87Sr/86Sr ratios were also converted to approximate salinity values using the two end-member salinity mixing model and uncertainty around salinity estimates was calculated based on propagated mixing model and laser ablation error. Finally, natal 87Sr/86Sr signatures were calculated by averaging all values within the core region of the otolith transect.

Otolith salinity profiles were plotted by year, and faceted by birth year, to show movement along the salinity gradient of the Umpqua River Estuary. Propagated instrumentation and data processing errors were plotted around salinity estimates. Next, mean natal isotopic signatures were plotted by birth year along with scaled and centered mean discharge at the USGS Elkton Gauge (USGS 2022) by water year, and a simple linear model was fit to test the effects of discharge on natal isotope signatures. Striped Bass are broadcast spawners with semi-demersal eggs, and typically spawn in fresh water with currents moving fertilized eggs downstream into productive and retentive brackish water habitats (Raney 1952; Moyle 2002). Given this, we assume that the Sr87/Sr86 ratios present in the core of each otolith we analyzed is generally representative of the location at which it was reared and first fed. Water-year encompasses October 1st of the previous year through September 30th of the subsequent year, and was selected to represent mean discharge because it more accurately reflects the hydrologic seasons in Oregon, where most precipitation typically falls in winter and spring.

Results

Otoliths from all 23 Striped Bass collected in the Umpqua River Estuary were prepared, aged, and analyzed for age specific Sr87/Sr86 isotopic ratios using laser ablation mass spectrometry. Age estimates by two authors were in agreement for 74% of otoliths after the first read and the remaining 26% were aged one year apart. In total, six year-classes were apparent representing years between 2008 and 2017. The two oldest fish analyzed were 11 years old and the two youngest were two years old when harvested in 2019.

Analysis of water samples for Sr87/Sr86 ratios found light freshwater signatures (0.7047) in the Umpqua River when compared to the freshwater portions of the Smith River (0.7074), the brackish to fully marine portions of the Umpqua Estuary (0.7049-0.7092), and the brackish to marine portions of Coos Bay and the Coquille River Estuary (0.7092). Given that the Umpqua River had a lower freshwater Sr87/Sr86 signature, a salinity mixing model was generated based on the isotopic gradient from the Umpqua River (Figure 3.3), with the assumption that low to moderate salinity values may also encompass the fresh-to-brackish portions of the Smith River. The resulting salinity mixing model shows relatively high certainty of salinity estimates at low salinity values (<5ppt), acceptable certainty at moderate salinity values (5-10ppt), and little to no certainty of predicted values at high salinity values (10+ppt; Figure 3.3A). As a result, predicted values based on strontium isotope ratios were close to what was observed at low salinity values and deviated from the prediction at high salinity values (Figure 3.3B). This pattern is consistent with previous studies which were unable to accurately reconstruct migratory dynamics in relation to salinity at values >10ppt using strontium isotopic ratios (Hobbs et al. 2019, Sellheim et al. 2022).

The distinctness of the strontium isotope signature in fresh and brackish portions of the Umpqua River allowed for determination of approximate rearing locations. Mean isotopic rearing signatures were plotted, by birth year, and fish were assumed to have reared in the fresh-to-brackish portions of the Umpqua River if Sr87/Sr86 ratios were below a threshold value of 0.7070, based on the minimum measured valued of ~0.7074 in the Smith River (Figure 3.4). The approximate location of the 0.7070 Sr87/Sr86 ratio at the time of water collection is shown as a red bar in Figure 3.1, with sites upstream having a Sr87/Sr86 ratio less than 0.7070. It is important to note this location is approximate, not fixed, and will move up or downstream based on inflow and tidal state.

In total, 12 out of 23 Striped Bass were determined to have reared in the fresh or brackish portions of the Umpqua River, with the remaining ten fish reared either in the higher salinity portions of the Umpqua River Estuary or in the Smith River (Figure 3.4). Concurrent plotting of scaled and centered mean annual discharge of the Umpqua River at Elkton, Oregon, did not show any apparent associations between flow and rearing location. A simple linear model testing the effect of scaled and centered mean annual discharge on mean natal Sr87/Sr86 ratios did not detect a relationship ($p=0.259$).

Striped Bass movement histories, in relation to salinity, displayed low incidences of movement from either low salinity (0.5-5ppt) portions of the Umpqua River Estuary or the freshwater portion of the Smith River (Figure 3.5). In addition, individual cohorts of fish appeared to remain somewhat grouped with few exceptions. There was little evidence of ocean movements, with the exception of an age-one Striped Bass from the 2015 cohort, and an age-zero and an age-three Striped Bass from the 2016 cohort. The age-zero and age-one Striped Bass both showed estimated salinity values of 9-12 ppt in 2016 and the age-three Striped Bass had estimated salinity values of 6.3-6.9 ppt in 2018, but with propagated measurement uncertainty encompassing full seawater (30+ ppt; Figure 3.5). Uncertainty in salinity estimates was high above 5ppt due to inclusion of instrumentation error in addition to propagated error in the salinity mixing model. On the other end of the salinity spectrum, movement into fully freshwater portions of the Umpqua River were uncommon after approximately one year of age (Figure 3.5).

Discussion

Our analyses revealed relatively little movement behavior out of the Umpqua Estuary and Smith River, strong distributional groupings in relation to salinity amongst year classes, rearing in both the freshwater portions of the Umpqua River as well as the brackish Umpqua Estuary and/or fresh Smith River, and recruitment at a much higher rate than had been previously documented for this system. The Umpqua Estuary Striped Bass population appears to currently be self-sustaining, with no evidence of strong metapopulation dynamics.

Our data indicate that, although movement to the Umpqua Estuary from the San Francisco Estuary and other systems is possible through oceanic movements, it is likely not driving the persistence of the population. While several individuals had salinity estimates encompassing seawater during 2016 and 2018, it is not clear whether these were forays into the Pacific Ocean or into the lower reaches of the Umpqua Estuary due to high uncertainty in salinity estimates over 5ppt. Theoretically, individuals could have migrated from the San Francisco Estuary since the 750km journey could be undertaken in approximately two weeks based on published movement speeds of Striped Bass on the Atlantic Coast (59km/d; Callihan et al. 2015). However, given the young age of most individuals (0 to 3 years) and the large average size of oceanic individuals on both the Pacific (Bennett and Howard 1997) and Atlantic (Secor and Piccoli 2007) Coasts, we find it unlikely that the high salinity individuals in our study represent immigrants from the San Francisco Estuary.

While we did not demonstrate any current incidences of immigration, it is important to note that immigration likely has played an important role in the persistence of the Umpqua Estuary Striped Bass population in the past and may increase in importance in the future as conditions evolve under climate change. For example, higher genetic diversity in the Umpqua Striped Bass population versus the nearby Coos Bay population, which suffered a population collapse and high incidences of pathogenic hermaphroditism (Waldman et al. 1998), may indicate a historically higher incidence of immigration to the Umpqua Estuary from the more genetically diverse San Francisco Estuary population. This trend may continue into the future, as Striped Bass from the San Francisco Estuary have been detected more frequently in the

Pacific Ocean during El Niño years, when water conditions are warm (Radovich 1963; Bennett and Howard 1997). El Niño events are expected to increase in both frequency and intensity under climate change (Wang et al. 2017), which may result in higher rates of movement of San Francisco Estuary Striped Bass into the Pacific Ocean and South Oregon Estuaries.

The strong distributional groupings in relation to salinity amongst Striped Bass within the Umpqua Estuary and Smith River indicates a relatively narrow span of preferred and/or optimal habitats within the system. Adult Striped Bass are known to migrate widely in search of food and/or suitable conditions (Raney 1952; Coutant 1985); therefore, the relatively narrow distribution of individuals indicates high productivity and abiotic suitability in the Umpqua Estuary and Smith River relative to other nearby habitats. This habitat suitability extends to larval and juvenile Striped Bass as well, as natal isotopic signatures were dispersed throughout the fresh and brackish portions of the estuary, independent of outflow conditions.

The recent apparent increased productivity of the system is further supported by the consistency of successful recruitment. The identification of six distinct year classes within ten years demonstrates consistent recruitment in a system which has historically had only infrequent recruitment events (Mullen 1974, Mullen 1977, Johnson et al. 1986). This consistent recruitment success may indicate that habitat conditions have improved for Striped Bass in the Umpqua Estuary, which is supported by anecdotal reports of an improved fishery by recreational anglers in recent years (ODFW 2022).

The cause of increased recruitment success amongst Umpqua Estuary Striped Bass is unclear. Possible explanations are improved water quality conditions as a result of changes in land use or discharge, improved rearing conditions due to habitat restoration, or a change in flow and temperature conditions due to climate change or altered dam operations. We are unable to fully investigate the effects of these potential drivers with our data; however, they warrant further investigation not only to determine the current and future suitability of the Umpqua Estuary for Striped Bass but to also determine the effects of altered conditions and an increased Striped Bass population on native fishes.

Consistent recruitment success of Striped Bass in the Umpqua Estuary has several implications for fisheries management. Striped Bass represent a culturally and economically important recreational fishery in the Umpqua Estuary, so increased recruitment success will undoubtedly result in benefits to the Striped Bass fishing community. However, concern has also been raised about the potential impacts of predation by Striped Bass on native salmonid populations (Gray 2005). Studies have revealed potential impacts of Striped Bass predation on outmigrating anadromous salmonids (Johnson et al. 1992), and the Oregon Department of Fish and Wildlife removed all take restrictions on Striped Bass in 2019 in an effort to reduce predation effects. The effects of this regulation change are not yet evident but may result in changes to the age structure and overall abundance of the Umpqua Estuary Striped Bass population.

It should be noted that our reliance on a relatively limited sample size, collected without representation of the full spatial extent of the estuary, limits interpretation of our results. For example, our identification of six year classes in a ten year period can only be considered a minimum, as younger fish may not have been accessible to the fishery given gear targeted towards larger individuals. Additionally, the lack of obvious coastal migrants amongst our samples does not disprove immigration and a functional metapopulation. A metapopulation encompassing the San Francisco Estuary and the Umpqua Estuary is still possible and may become more important as oceanic conditions evolve given climate change.

Finally, since sex was not recorded, it is possible that the lack of observed immigration was due to male bias in our samples, given that females are most likely to be found in the coastal environment (Scofield 1931). This is possible, however, older Striped Bass (>age 6) tend to skew female (Setzler et al. 1980) and our sample does include four individuals over seven years of age, increasing the likelihood that at least some females were included.

Conclusion

Our study demonstrates continued persistence of a naturally established yet non-native population of Striped Bass in the Umpqua Estuary. Data show consistent local recruitment of Striped Bass in this system and no evidence of immigration from the San Francisco Estuary. The consistency of local production as evidenced by six distinct year classes, in a system that historically only sporadically supported successful recruitment, demonstrates a change in local conditions that will likely result in increased fishing opportunity and potentially increased predation pressure on native fishes. Additionally, the spatially narrow distribution of fish in our study, which was primarily restricted to the low-salinity and/or fresh Smith River portions of the Umpqua Estuary, means that fishing opportunity and predation will likely be restricted to a relatively small portion of the system. This spatial distribution will limit predation effects on outmigrating salmonids; however, differential rearing strategies and outmigration timings will produce non-equal effects on various species and run types. Monitoring of Striped Bass abundance and seasonal diets is needed to quantify any potential effects.

Finally, the lack of an obvious metapopulation implies that it is unlikely that the Umpqua Estuary is functioning as a sink to the larger San Francisco Estuary population of Striped Bass. These populations appear to exist somewhat independently, although, emigration from the San Francisco Estuary to the Umpqua and other Oregon Estuaries has been demonstrated in the past, possibly under different oceanic and estuarine conditions. As conditions in the Pacific Ocean change as the climate changes, including the predicted increase in the frequency of extreme El Niño events (Wang et al. 2017), it is possible that coastal movements of Striped Bass may become more important in the future. Future studies should examine a larger sample size of individuals for evidence of immigration and/or employ active monitoring techniques such as acoustic telemetry to determine the extent of immigration.

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Figures

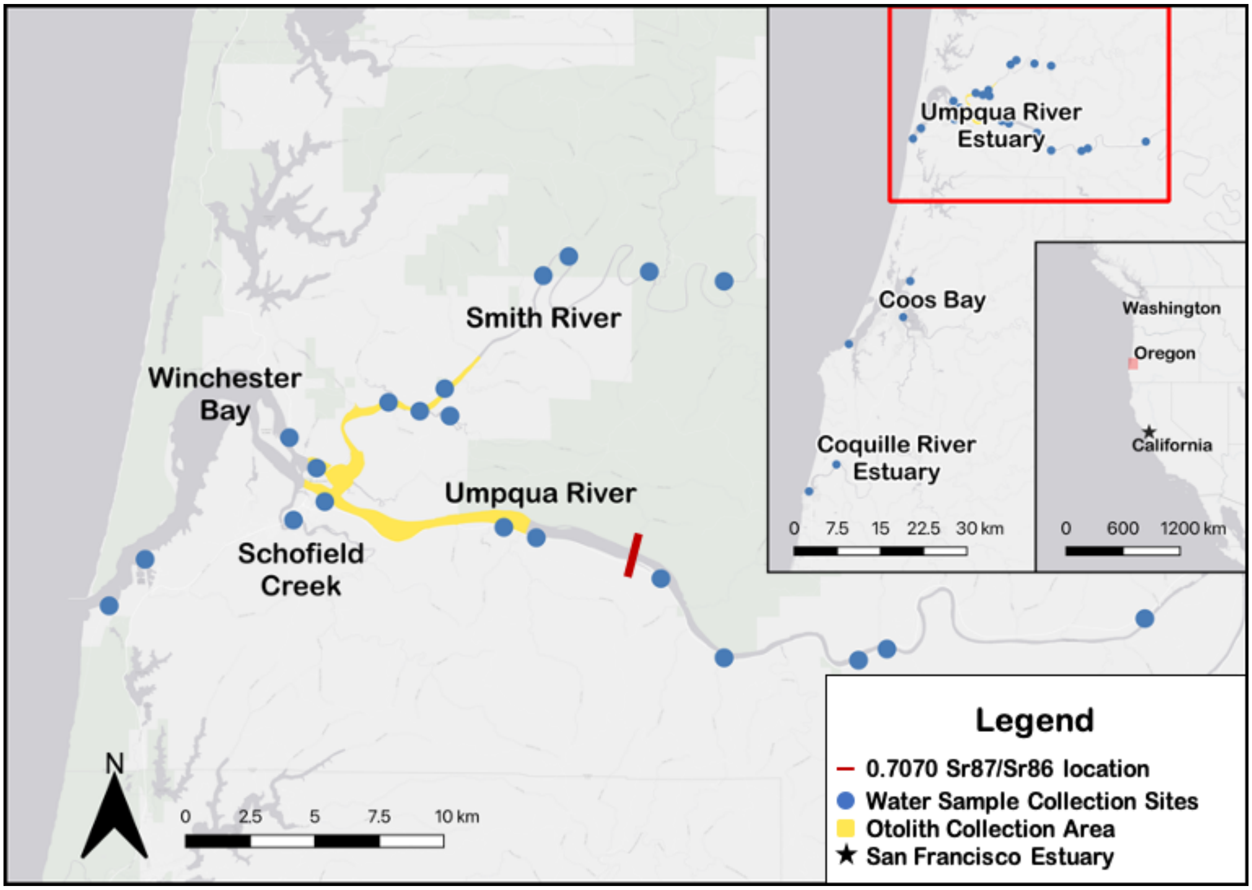

Figure 3.1. Map of Umpqua Estuary, with insets of Southern Oregon Coast and Pacific Coast of North America. Red bar represents approximate location of 0.7070 Sr87/Sr86 ratio at time of water collection, blue circles represent water sample collection sites, yellow shaded region represents area where Striped Bass Otoliths were collected, and black star is the San Francisco Estuary.

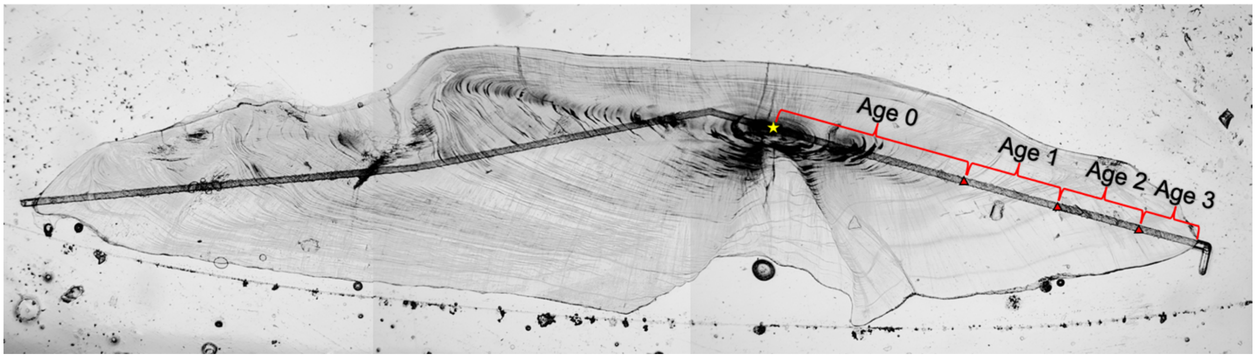

Figure 3.2. Cross section of Striped Bass otolith. Dark line running left to right is the laser ablation burn scar, yellow star represents the core, red triangles are placed on annual bands along burn scar, and ages 0 through 3 are labeled along burn scar.

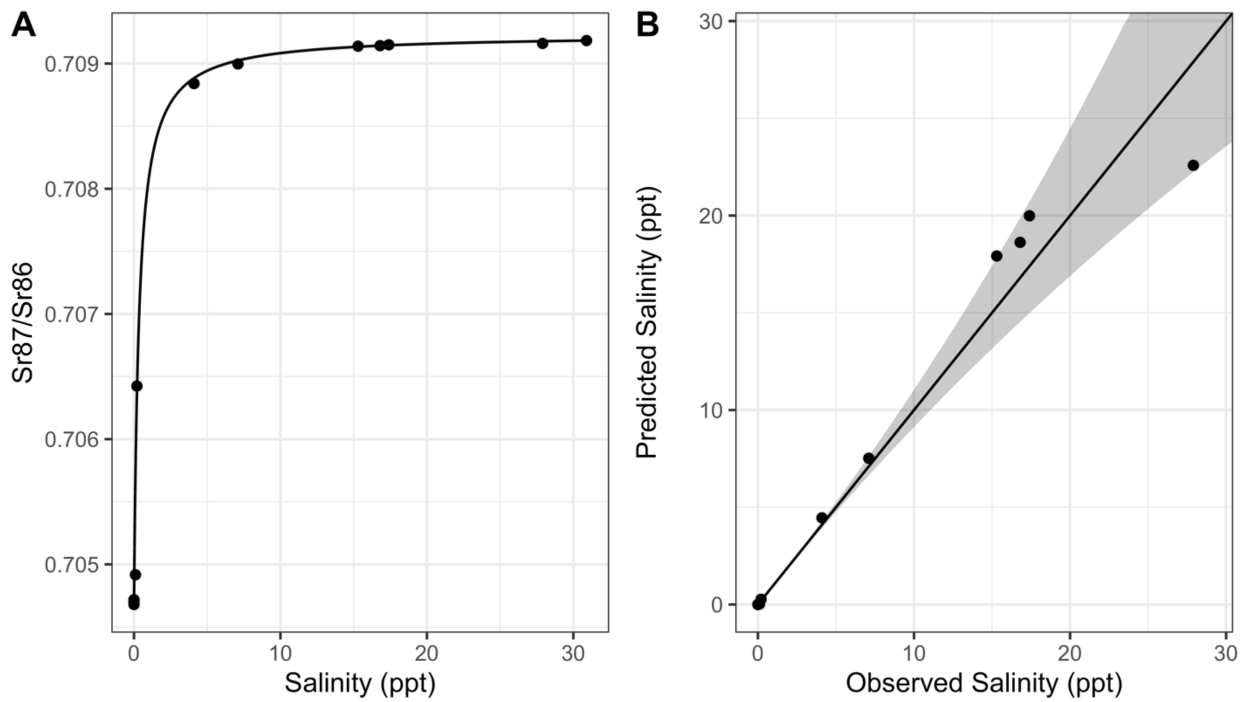

Figure 3.3. Panel A: Strontium 87/Strontium 86 (Sr87/Sr86) salinity mixing model for Umpqua Estuary, Oregon. Panel B: Predicted salinity (ppt) from the mixing model versus observed salinity from water samples. Points in both plots represent actual salinity and Sr87/Sr86 values from water samples.

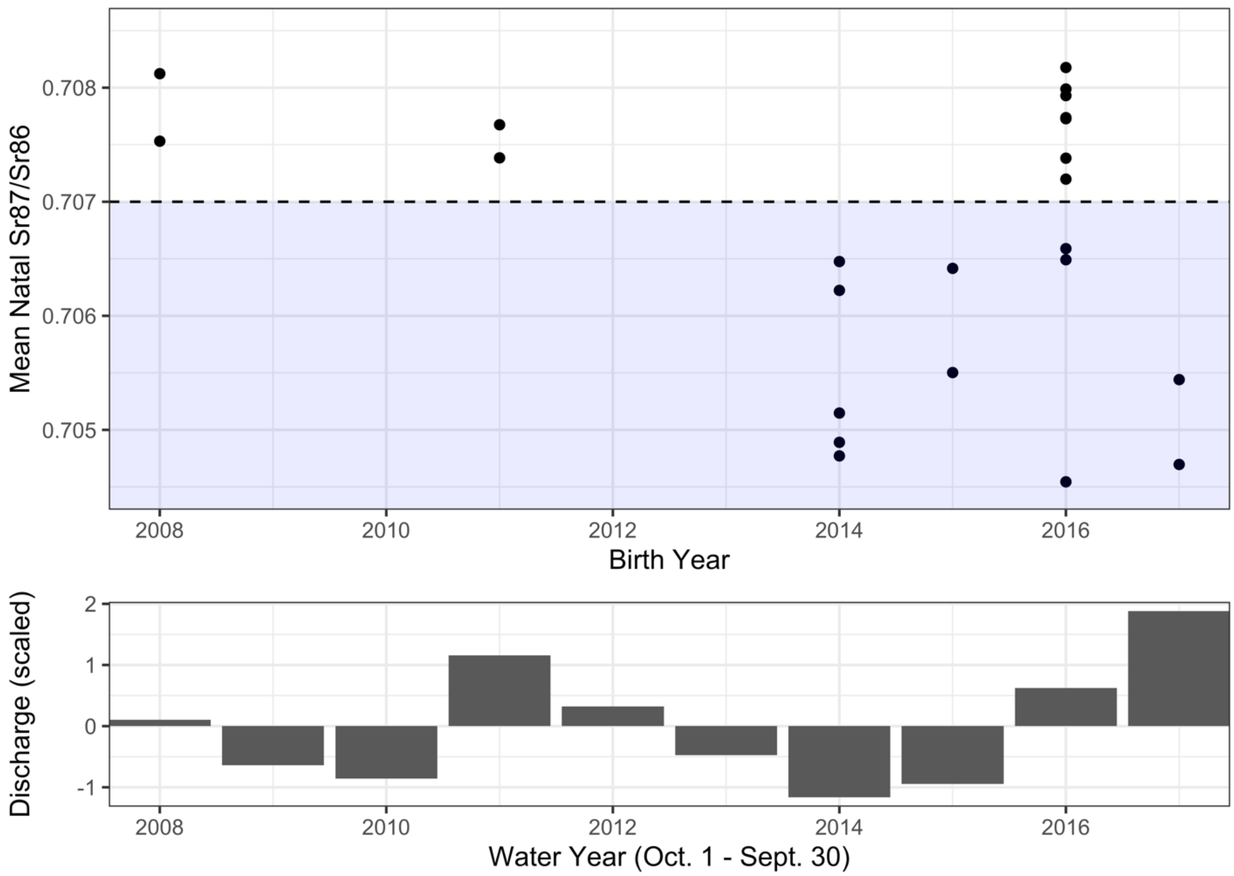

Figure 3.4. Top: Mean Strontium 87/Strontium 86 (Sr87/Sr86) isotopic signatures within otolith core (natal) region by birth year for Striped Bass collected in the Umpqua Estuary in 2019. Blue shaded region below dotted line represents isotopic signatures within the fresh Umpqua River, unshaded region above line represents brackish Umpqua Estuary or fresh Smith River signatures. Bottom: Scaled and centered discharge by water year (Oct. 1 to Sept. 30) in the Umpqua River at Elkton, Oregon.

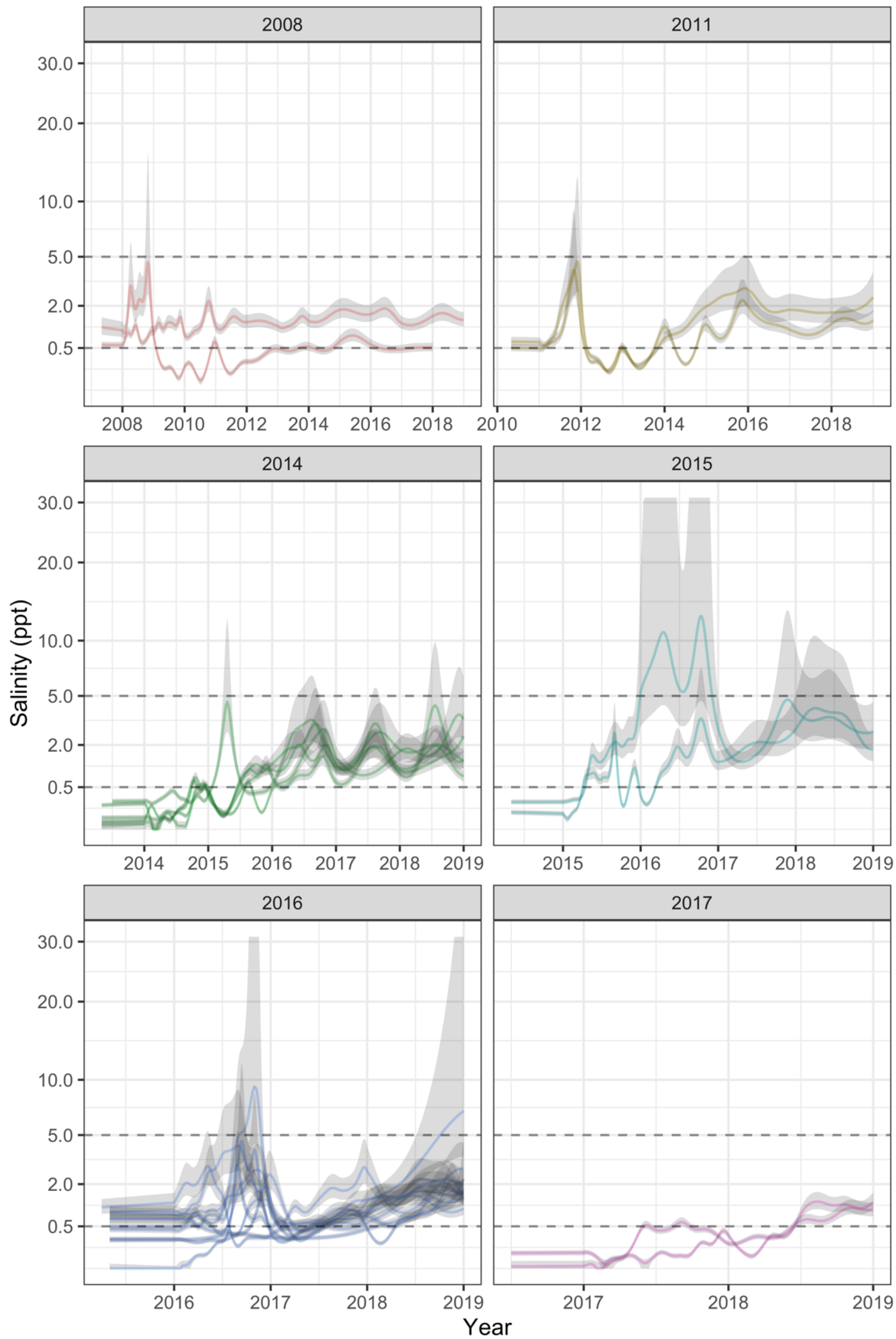

Figure 3.5. Migratory histories in relation to salinity by birth year of Striped Bass collected in the Umpqua Estuary, Oregon. Solid lines represent salinity estimates and shaded grey area

represents propagated uncertainty around estimates. Values below horizontal dotted line at 0.5ppt represent Umpqua River water, values between 0.5 and 5ppt represent brackish portions of the Umpqua Estuary, and values above horizontal dotted line at 5ppt have considerable uncertainty associated with salinity estimates.