RESEARCH

Wakasagi in the San Francisco Bay Delta Watershed: Comparative Trends in Distribution and Life-History Traits with Native Delta Smelt

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ABSTRACT

Intentional introductions of non-native fishes can severely affect native communities. Wakasagi (*Hypomesus nipponensis*, referred to as Japanese Pond Smelt) are native to Japan and were once separated from their non-native congener the endangered Delta Smelt (*Hypomesus transpacificus*) of the San Francisco Estuary (hereon "estuary") of California. Wakasagi were introduced into California reservoirs in the 20th century as

forage fish. Wakasagi have since expanded their distribution downstream to the estuary, but less is known about Wakasagi's current distribution status, biology in the estuary, and negative influences on Delta Smelt. In this study, we took a comparative approach by synthesizing long-term field monitoring surveys, modeling environmental associations, and quantifying phenology, growth, and diets of Wakasagi and Delta Smelt to describe abundance and range, trends of co-occurrence, and shared ecological roles between smelt species. We found Wakasagi in greatest abundance in the upper watershed below source reservoirs, and in the northern regions of the estuary with the most co-occurrence with Delta Smelt; however, their range extends to western regions of the estuary, and we found evidence of an established population that annually spawns and rears in the estuary. We found these smelt species have similar ecological roles demonstrated by overlaps in habitat use (e.g., an association with higher turbidities and higher outflow), phenology, growth, and diets. Despite similarities, earlier hatching and rearing of Wakasagi during cooler months and reduced growth during warmer drought years suggest this species is unlike typical non-natives (e.g., Centrarchids), and they exhibit a similar sensitivity to environmental variability as Delta Smelt. This sensitivity may be why Wakasagi abundance remains relatively low in the estuary.

KEY WORDS

Wakasagi, ecology, distribution, life history, Delta Smelt

INTRODUCTION

Human-mediated species introductions can have severe unintended consequences on biodiversity, food webs, and ecosystem processes through competition, predation, and parasitism, (Erarto and Getahun 2020; Mayfield et al. 2021) and is considered the second greatest threat to global biodiversity behind habitat alteration (Simberloff et al. 1997; Hobbs 2000). The effect of invasive species can be enhanced profoundly when introduced species interbreed with native species, and in cases where hybridization occurs with native species in low abundance rapid extinction is likely (Huxel 1999; Rhymer and Simberloff 1996). Recently, as a result of climate change, the effect of invasive species through hybridization with natives has accelerated (Muhlfeld et al. 2014). Together, the effects of invasive species are predicted to be greater in aquatic ecosystems such as rivers, lakes, and coasts as compared to terrestrial ecosystems because freshwater ecosystems have the highest concentration of species per surface area of any other habitat (Thomaz et al. 2015).

The San Francisco Estuary (estuary) of California, along the eastern coast of the Pacific Ocean, is a highly invaded ecosystem (Cohen and Carlton 1998). Many invasive species in the estuary have been introduced intentionally for pest control, recreation, or as prey for native species (Dill and Cordone 1997); however, many introductions in the estuary occur unintentionally through ballast water exchange and releases of ornamental aquarium species (Cohen and Carlton 1998; Minchin and Gollasch 2002). Such introductions have profoundly affected the ecology of the estuary. For example, unintentional introductions of invertebrates such as the benthic clam corbicula (*Corbicula fluminea*) and the overbite clam (*Potamocorbula amurensis*) have severely reduced plankton densities in the estuary, correlated with major declines of native fishes (Kimmerer et al. 1994; Feyrer et al. 2003; Mac

Nally et al. 2010; Crauder et al. 2016). Intentional introductions of recreationally and commercially important fishes such as Striped Bass (*Morone saxatilis*) and Largemouth Bass (*Micropterus salmoides*) have contributed to declines in native fish species via predation (Lindley and Mohr 2003; Nobriga and Feyrer 2007; Loboschefsky et al. 2012; Sabal et al. 2016; Nobriga and Smith 2020); whereas intentional introductions of Mississippi Silversides (*Menidia audens*) and Threadfin Shad (*Dorosoma petenense*) for pest control and as freshwater forage fish, respectively, may have led to increased resource competition with native fishes in the estuary (Feyrer et al. 2003; Bennett 2005; Mahardja et al. 2016). As of the late 1990s, 234 invasive species had been identified in the estuary, 30 of which were non-native fishes (Cohen and Carlton 1998), and it's expected these numbers have increased substantially in recent years.

One non-native fish of interest in the estuary is the Wakasagi, also commonly referred to as the Japanese Pond Smelt (*Hypomesus nipponensis*, hereon "Wakasagi"). Wakasagi are widely distributed from the Kuril Islands of Russia and coastal regions and lakes of Japan to the South Korean Peninsula (Katayama et al. 2001; Ilves and Taylor 2008; Choi and Kim 2019). In Japan, Wakasagi support a commercial freshwater fishery supported by an aquaculture program with annual hatchery releases of >10 billion eggs and newly hatched larvae into lakes and reservoirs (Nakamura and Watanabe 2001). In 1959, the California Department of Fish and Game (CDFG) transported 3.6 million Wakasagi eggs from Japan for intentional stocking in upper California reservoirs and streams to serve as forage fish for cold-water Trout and Salmon (Wales 1962; Dill and Cordone 1997). With reservoir releases, Wakasagi moved down the watersheds and started to be detected in estuary monitoring. By 1975, detections of Wakasagi occurred in the upper Sacramento River, and by 1995, they were detected throughout the larger Sacramento area and American River (Aasen et al. 1998). Wakasagi are now caught throughout the estuary, although much about their life-history and population status in the estuary remains

uncertain, and abundance and distribution may be limited.

In the estuary, Wakasagi are caught in monitoring surveys alongside the critically endangered congener Delta Smelt (*Hypomesus transpacificus*), indicating similarities in habitat use and potentially overlapping ecological niches. Delta Smelt is a pelagic species endemic to the estuary and—following their threatened and endangered listings under the Federal and California Endangered Species Acts, respectively (Fed Regist 1993; CFGC 2009)—became one of the most highly monitored fish in California as a result of their large role in management of state water resources. Despite their listing and subsequent management actions to help the species, Delta Smelt have continued to decline, with a strong possibility of extinction in the near future (Hobbs et al. 2017). Understanding the effects of non-native species such as Wakasagi can provide new insights into the demise and protections of Delta Smelt. For example, non-native Mississippi Silversides share similar life-history traits as Delta Smelt and compete for resources (Bennett 2005; Moyle et al. 2016). Additionally, genetic analyses have identified that Delta Smelt and Wakasagi can hybridize (Trenham et al. 1998; Fisch et al. 2014; Benjamin et al. 2018), with progeny being visually indistinguishable from Delta Smelt (Wang et al. 2005), which complicates monitoring efforts. In addition, both species < 50 mm can be challenging to speciate in the field which may lead to misidentification and inaccurate population assessments of Delta Smelt (Benjamin et al. 2018; Jenkins et al. 2020).

While the ecology and life-history of Delta Smelt in the estuary (see review Moyle et al. 2016), and Wakasagi in Japan, have been well studied, research into the estuary's Wakasagi has been limited to topics of morphology, genetics, and physiology (Swanson et al. 2000; Wang et al. 2005; Wang 2007; Fisch et al. 2014; Benjamin et al. 2018). Morphologically, Wakasagi are of similar size and appearance to Delta Smelt, with few distinguishing external traits helpful for speciation (Wang et al. 2005), making genetic confirmation of field-identified individuals a

necessity at times (Benjamin et al. 2018). Both species are primarily annual (some live 2 years), reaching sexual maturity in their first year, and spawning in freshwater during late winter to early spring (Katayama et al. 1998, 1999; Katayama and Kawasaki 1994; Katayama 2001; Bennett 2005). However, otolith analyses of Delta Smelt suggest that some portion of the population may spawn in or near brackish water (Bush 2017; Hobbs et al. 2019). Both Wakasagi and Delta Smelt consume similar prey composed primarily of pelagic zooplankton (Yamanaka and Kuwabara 2000; Slater and Baxter 2014; Mahardja et al. 2019) and exhibit similar life-history strategies (Katayama et al. 2000, Katayama 2001; Moyle et al. 2016; Hobbs et al. 2019). Physiologically, a laboratory study demonstrated that Wakasagi have relatively higher tolerances of temperature and salinity than Delta Smelt (Swanson et al. 2000), suggesting Wakasagi could be pervasive throughout the estuary, but the extent of their distribution and abundance is uncertain.

In this study, we summarized long-term catch data of Wakasagi and Delta Smelt from multiple monitoring surveys and compared the species distribution in the estuary as well as growth, phenology, and diets within the Yolo Bypass, a northern region of the estuary. Our goal was to synthesize information to better understand Wakasagi populations in the estuary and upper watershed and to identify potential overlap in ecological niches of Wakasagi and Delta Smelt. Specifically, our study questions are: (1) Do catch data indicate that Wakasagi abundance in the estuary is increasing? (2) Are Wakasagi increasing in spatial extent in the estuary? and (3) Do Wakasagi occupy an ecological niche similar to Delta Smelt? To quantify the distribution and abundance of the Wakasagi population in the estuary, we conducted a synthesis of catch data by compiling historical data sets from a series of fish-monitoring programs in the estuary by the California Department of Fish and Wildlife (CDFW) 20-mm Survey, Spring Kodiak Trawl, Summer Townet Survey, Fall Midwater Trawl, US Fish and Wildlife Service's (USFWS) Delta Juvenile Fish Monitoring Program (DJFMP), and other screw trap programs. These monitoring

programs sample across much of the watershed and utilize several different gear types, providing detail on a variety of habitat types. To investigate if Wakasagi and Delta Smelt have similar ecological niche characteristics, we conducted a comparative analysis of Wakasagi and Delta Smelt habitat associations and detection probabilities (abiotic factors) from the USFWS Enhanced Delta Smelt Monitoring Program, as well as assessed life-history trait overlap—including reproduction time, growth rates, and diets (biotic factors)—from the California Department of Water Resources (CDWR) Yolo Bypass Fisheries Monitoring Program (YBFMP). The characterization of similarities (or niche overlap) in ecology and life-history between these two species in the estuary is critical to better understand the potential for negative effects on Delta Smelt.

MATERIALS AND METHODS

Distribution and Catch Summaries

We evaluated Wakasagi range and catch in the estuary and upper watershed by summarizing historical field survey catch data from a variety of gear types, including rotary screw traps, beach seines, trawl surveys, and salvage from state and federal pumping facilities (Table 1, Figure 1). We analyzed the most current available full data sets for all surveys (at the time of analyses)— apart from both Stanislaus and Tuolumne rotary screw traps, where Wakasagi catch was zero and reported directly to the authors by the respective studies' project managers (2018 email between B. Davis and J. Guignard, unreferenced, see "Notes"). We analyzed all available data, but, aside from a single Wakasagi recorded by the Bay Study in 1982, there were no additional Wakasagi caught in any of the analyzed surveys until 1994 (Table 1); thus, we omitted years before 1994 in our assessments.

Data sets were obtained through the Environmental Data Initiative (EDI), File Transfer Portal (FTP) servers (CDFW) or data requests from individual monitoring programs (available upon request); see Appendix Table A1 for data sources, fisheries agencies, and programs. Catch data were

post-processed for quality, converted to catch per effort fished where possible, and analyzed using R (R Core Team 2019). Additional details of the monitoring programs and data analysis specific to the data sources, including major changes in sampling programs, are provided in Appendix A (Field Survey Methods) for the YBFMP and the DJFMP, with more information available in EDI metadata (versions including edi.233.2 and edi.244.4). CDFW sampling program metadata are provided through respective internet repositories (FTPs) or by contacting the corresponding author. Summaries of each gear type across monitoring programs are provided below.

Rotary Screw Traps

We assessed adult Wakasagi catch and range in channel habitat using catch and trap effort data for 8-ft (2.44-m)-diameter rotary screw trap locations in north Central Valley rivers and the northern Delta (Figure 1B). We used screw trap data from the Yolo Bypass Toe Drain southwest of Sacramento, CA near Prospect Slough (IEP et al. 2019), the lower American River at Isabelle Island near Sacramento, the Sacramento River near Knights Landing (river kilometer 144), and the Feather River between (approximately) Live Oak and Oroville. Most of the traps were either fixed in one location (Yolo Bypass) or moved within a relatively small area of a river reach (American River and Knights Landing); however, the Feather River trap was regularly moved to sample different sites along a stretch of river approximately 40 km in length. Time-span for screw trap data varied by location, with some beginning in 1998 (Yolo and Feather River) and others more recent in 2011 and 2013 (American River and Knights Landing) as described in Table 1. Traps were typically run seasonally (winter and spring), but this varies by agency (see Table 1). Because of differences in methodology between rotary screw trap programs, our results are solely intended to elucidate broad spatial and temporal trends in Wakasagi distribution and abundance, and not meant to make direct comparisons between screw traps. To control for differences in sampling effort over time, catch per unit effort (CPUE) for each trap was calculated for each calendar year as the total number of

Table 1 Survey data sets for trawls, beach seines, rotary screw traps and salvage. Total Wakasagi catch, maximum catch per year, and average fork length (FL) were calculated for each data set at the time data were accessed (*salvage adjusted by pumping and sampling time; see methods). Fish lengths are reported as FL except as noted by the superscript SL (standard length) or TL (total length), and NA (not applicable). CDWR's Yolo Bypass screw trap provided fish for otolith and diet analysis in this study from 2012–2016.

| Agency	Survey	Time of year (approx.)	Period of data accessed	Number of stations	Total Wakasagi	Max/year (calendar)	Average FL (mm)
CDFW	Fall Midwater Trawl	September–December	Sep 1967–Dec 2019	100 historic + 22 from 1990–2010	83	16	89
CDFW	Summer Townet	June–August	Jun 1959–Aug 2019	32 historic + 8 added in 2011	64	15	65
CDFW	20-mm	April–July	Apr 1995–Apr 2020	54	392	96	17
CDFW	Spring Kodiak Trawl	January–May	Jan 2002–Mar 2020	40 core stations + 38 intermittent	59	8	78
USFWS	Sacramento Midwater Trawl	April–September	Apr 1988–Sep 2019	1	25	8	61
USFWS	Sacramento Kodiak Trawl	October–March	Dec 1994–Dec 2019	1	449	104	63
USFWS	Chipps Island Trawl	Year round	May 1976–Dec 2019	1	53	9	90
USFWS	Mossdale Trawl	Year round	Apr 1994–Dec 2019	1	18	4	54
CDFW	Bay Study Otter Trawl	Year round	Jan 1980–Dec 2018	35 historic + 17 from 1988–1994	2	1	73
CDFW	Bay Study Midwater Trawl	Year round	Jan 1980–Feb 2018	35 historic + 17 from 1988–1994	8	2	85
UCD	Suisun Marsh Otter Trawl	Year round	May 1979–Sep 2018	21	13	5	71[SL]
UCD	Suisun Marsh Larval Sled	Year round	Apr 1994–Jun 1998	5	90	50	NA
UCD	Bay Tributary Otter Trawl	Year round	2015–2019	8–20	13	8	49[SL]
UCD	Bay Tributary 20-mm	March–June	2016–2019	8–16	2	1	36[TL]
CDFW	North Bay Aquaduct Survey	February–July	Feb 1992–Jun 2004	8	192	100	93
CDFW	Delta Smelt Larva Survey	January–July	Jan 2005–Apr 2007	19–49	347	273	10
CDFW	Smelt Larva Survey	January–March	Jan 2009–Mar 2019	44	20	5	8
USFWS	EDSM Kodiak Trawl	July–March	Dec 2016–Mar 2020	18–41	1405	859	70
USFWS	EDSM 20mm Survey	April–June	Apr 2017–Jun 2019	18–41	20	15	23
UCD	Suisun Marsh Beach Seine	Year round	Sep 1979–Jan 2020	3	11	4	60[SL]
CDWR	Yolo Bypass Beach Seine	Year round	Jan 1998–Mar 2020	14	32	13	41
USFWS	Beach Seine Survey	Year round (varies)	Mar 1976–Dec 2019	58	4550	2661	50
CDFW/ USBR	Salvage	Year round	Jan 1981–Apr 2020	2	4246*	2301*	NA
CDWR	Yolo Bypass Screw Trap	December–June	Jan 1998–Mar 2020	1	241	87	44
CDWR	Feather River Screw Trap	December–June	Dec 1998–Jun 2019	1	249980	110666	61
CDFW	Knight's Landing Screw Trap	October–June	Oct 2011–Jun 2019	1	99	83	43[TL]
CDFW	American River Screw Trap	Year round (varies)	Jan 2013–May 2018	1	6431	2723	61
CDFW	Yuba River Screw Trap	Year round (varies)	Nov 1999–Aug 2009	1	4	2	79
USFWS	Stanislaus Screw Trap (Caswell)	January–June	Feb 1996–Apr 2020	1	0	0	NA
USFWS	Stanislaus Screw Trap (Oakdale)	December—June	Apr 1993–Apr 2020	1	0	0	NA
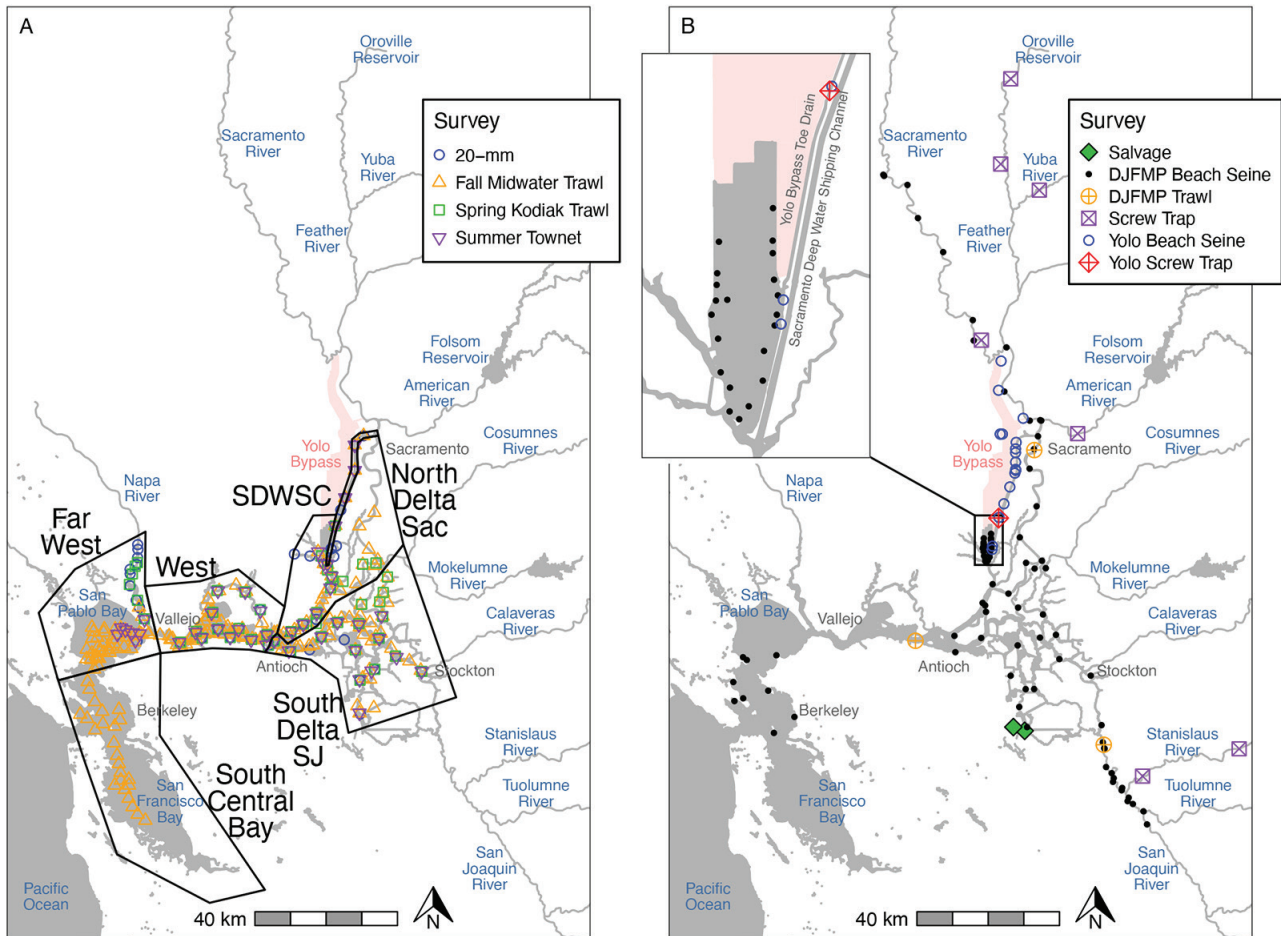
Figure 1 Maps of the San Francisco Bay-Delta Estuary. (**A**) Four long-term CDFW monitoring surveys and region assignments used for the comparative Delta Smelt and Wakasagi analysis (Figure 3). For historical context, all sampling locations represented in Table 1 are shown (exclusive of locations without available coordinates). This may include locations that have been sampled routinely over time, sampled intermittently, or discontinued. (**B**) Sampling locations for a subset of additional surveys used to assess Wakasagi catch, as well as Yolo Bypass surveys used to assess life-history traits including growth, phenology, and diet.

Wakasagi caught per total number of hours a trap was actively fished (Wakasagi catch hr^{-1}). We grouped data by year and removed any missing effort data (NA or zero hours fished).

Beach Seines
Beach seine catch and sampling effort data from the YBFMP (1998-2020; IEP et al. 2019) and the DJFMP (1976-2019; IEP et al. 2020) were used to assess juvenile and adult Wakasagi abundance and distribution in shallow, unobstructed habitat within the San Francisco Bay-Delta region (Table 1, Figure 1B). The northeast Delta, on the Sacramento River floodplain in the Yolo Basin, is

covered by YBFMP beach seine sampling, while the rest of the Bay-Delta region—from littoral zones within San Pablo Bay to the lower San Joaquin River—is covered by DJFMP beach seine sampling. We grouped data by year and removed any missing effort data (NA or zero volume sampled). To control for differences in sampling effort, we calculated CPUE for beach seining for each year as Wakasagi per cubic meter of water sampled (Wakasagi catch m^{-3}).

Trawls
We summarized data from 19 different trawl surveys in the estuary to assess the general range

and catch of Wakasagi in pelagic habitat (see Table 1). We then used four long-term CDFW trawl surveys (20-mm survey, Spring Kodiak Trawl survey [SKT], Summer Tow Net survey [STN], and Fall Mid-Water Trawl survey [FMWT]) to compare range and catch data for different life-history stages of Wakasagi and Delta Smelt (Figure 1A). The spatial and temporal scopes within and between these surveys vary, with some surveys starting as far back as the 1950s and others as recently as 2009; some surveys cover the entire estuary, while others focus solely on smaller regions such as Suisun Marsh or the Yolo Bypass. We grouped stations into six regions defined by several of the longer-running surveys (Figure 1A). Not all surveys have the same spatial scope, so some regions are absent from certain surveys. The south and central bay region encompasses the higher-salinity area of the San Francisco Bay south of San Pablo Bay. The far west region encompasses San Pablo Bay and the Napa River estuary. The west region encompasses Carquinez Strait to Suisun Bay/Marsh. The South Delta/San Joaquin River region encompasses upstream of the mouth of the San Joaquin River, east toward the Mokelumne River and southeast toward the Delta pumping facilities. The North Delta/Sacramento River region encompasses areas northeast, upstream of the mouth of the Sacramento River, and including the Cache Slough complex. Finally, the Sacramento Deep-Water Ship Channel (SDWSC), a manmade terminal side-channel of the lower Sacramento River—which is unique hydrologically from other areas of the Bay-Delta—was treated as another region.

To compare Wakasagi and Delta Smelt catch trends over time, we focused on years from 1994 on, because this is when Wakasagi first appear consistently in catch data within the Delta. Furthermore, as many of these surveys have gathered data over many years, they have often added or removed stations, altered sampling frequency or duration, and made changes to gear. Accounting for so many variables makes it difficult to directly compare catch data between surveys, and programmatic changes (such as adding or removing stations) may limit the scope of spatio-temporal analyses of individual surveys. Therefore, we took a two-step approach to characterizing Wakasagi catch in the Bay-Delta. The first approach summarized total Wakasagi catch per survey to identify which surveys were most likely to catch Wakasagi (Table 1). The second approach was a more detailed investigation of the catch and range of Wakasagi and Delta Smelt for select surveys (as the annual mean catch per tow for regions of the Bay-Delta; Figure 1A). Our purpose for this analysis is to characterize broad spatial and temporal trends in Wakasagi (and Delta Smelt) distribution and abundance, not to make direct comparisons between trawl surveys.

Trawl surveys in the Bay-Delta were conducted year-round, with certain surveys done at specific times of year to target different life-history stages of fishes. To control for differences in sampling effort over time, we calculated CPUE for each survey for each year as the total number of Wakasagi caught per trawl net tow (Wakasagi catch/tow).

Salvage

A main component of water management in California is water diversions from state and federal pumping facilities in the South Delta (Figure 1B). Water exports through these facilities can lead to entrainment of fishes into the Central and South Delta. Fish salvage monitoring documents the salvage of fishes to estimate the effects on species populations such as Delta Smelt. Two salvage data sets spanning 1981–2012 and 2012–2020 were first merged, after which rows with no data (NA) for species code or count were removed. Old and new state pumping facilities were combined into a single "State Facility" category to compare with the federal pumping facility, and data were truncated to begin in 1994, when the first Wakasagi were detected in Delta salvage operations. Data were categorized and grouped by year, volume of water pumped was converted from acre-feet (AF) to cubic meter (m^3) and CPUE was calculated for each water year for state and federal pumping facilities. CPUE was standardized for sampling effort with the following equation:

$$CPUE = \frac{\left(\frac{Minutes\ pumping}{Sample\ time\ length}\right) \times Count}{\left(\frac{m^3}{water\ year}\right)}$$

Length Frequency

We assessed the ability of gear types (larval trawls, beach seines, rotary screw traps, and mid-water trawls) to target Wakasagi life-stages by analyzing length frequency distributions by survey type. Currently Wakasagi are unintentionally caught and not a target species of any long-term monitoring programs, as compared to some surveys that specifically target Delta Smelt or Chinook Salmon (*Oncorhynchus tshawytscha*). Data were compiled from data sets used in catch and range (abundance and distribution) analyses, which included fish length data (Table 1). A few surveys recorded fish length in standard or total length, but these were a very small number of fish compared to surveys recording fork length and would little affect length analysis. Nonetheless, as an approximation derived from Wakasagi morphometric data (Saruwatari et al. 1997; Jenkins et al. 2020), survey data in standard length or total length were multiplied by a factor of 1.08 or 0.92, respectively, to convert to fork length before analyses.

Comparative Life-History Traits
Occupancy Model-Enhanced Delta Smelt Monitoring Data

To assess and compare the habitat associations of Wakasagi and Delta Smelt to commonly measured water quality parameters, we used data from the Enhanced Delta Smelt Monitoring program (EDSM). The EDSM is a fish monitoring program initiated by the U.S. Fish and Wildlife Service (USFWS) in late 2016 to provide a finer spatio-temporal resolution of Delta Smelt abundance and distribution (USFWS, Johnston, et al. 2020). Data from the EDSM are well suited for habitat modeling in a few ways. The EDSM uses a stratified random sampling design (Stevens and Olsen 2004), which allows the data to adhere better to the common model assumption of independence. The program also conducts replicate tows at each site, which can be used to account for the imperfect detection that underlies almost all monitoring data. Lastly, the EDSM data represent one of—if not the most—comprehensive data sets on Delta Smelt within the estuary in

recent years, with sampling that occurs across multiple geographic strata for 4 days a week, year-round. The number of strata has ranged from four to ten, and the number of sites per stratum per week has ranged from two to six. When Delta Smelt are large enough to identify in the field (Phases 1 and 3; see below) the number of replicate tows per site is constrained between two and a maximum that has changed over time but generally falls between four and ten; within this range, sampling stops after one or more Delta Smelt have been caught, when applicable.

Sampling for EDSM has three phases that correspond to Delta Smelt life stages. Phase 1 samples adults using Kodiak trawls from approximately December through March, corresponding to the Delta Smelt spawning season. Phase 2 samples post-larvae and small juveniles using larval tow nets from approximately April through June. Phase 3 samples juveniles and sub-adults using Kodiak trawls from approximately July through November. Sampling during Phase 2 has been less consistent as a result of multiple gear comparison studies conducted in 2 out of the 3 years when data were available to us. As such, we focused our analysis on data just from Phases 1 and 3, which consistently used the same gear. In this study, we were able to include data from the very first phase of EDSM, Phase 1 of 2016 (December 2016–March 2017), to Phase 3 of 2019 (July 2019–November 2019). We removed data from the southern Delta and upper Sacramento River because these areas were not sampled consistently throughout the study period (see Figure A1 for spatial distribution of final data). For more details on EDSM protocols, see USFWS, Johnson, et al. (2020).

We used an occupancy model framework (MacKenzie et al. 2002; MacKenzie et al. 2006) to examine factors that may affect the occurrence and detectability of Wakasagi and Delta Smelt. A standard application of occupancy modeling calls for conducting replicate surveys at a given site over time and recording whether or not the focal species was detected during each survey. This information is used to construct a model likelihood based on the probability

that a given site is occupied and the probability that the species was detected during a survey, conditional on the site having been occupied. The assumptions underlying this model are that (1) the occupancy status of a site does not change over the period during which the replicate surveys are conducted (closure assumption); (2) occupancy and detection probabilities are either constant, or differences are fully accounted for with model covariates at the site level (occupancy) or site–survey level (detection); and (3) detections between replicate surveys at a site and between sites are independent (MacKenzie et al. 2006).

We applied this framework to EDSM by treating replicate tows at a site as replicate surveys and defining a catch of at least one fish in a tow as a detection. We included covariates in the occupancy and detection sub-models using a logistic function. Occupancy models are typically fit with data collected as part of a dedicated occupancy study, and, historically, occupancy studies have focused on terrestrial species whose habitat can be divided into well-defined sites. As such, fitting occupancy models with data from an aquatic monitoring program represents an opportunistic use of data.

For the detection probability sub-model, covariates tested for each species include categorical dummy variables for cohort year (year in which each osmerid cohort was born), region (see Figure A2), Secchi depth, and the direction of the tow (upstream or downstream). Region reflects a coarse spatial partitioning of the estuary without introducing an excessive number of coefficients. We included cohort year and region to account for large-scale spatio-temporal variability with the expectation that higher (lower) abundance equates to higher (lower) detection probability. Secchi depth (in meters) was included as a covariate for the detection sub-model based on the findings of a previous study (Peterson and Barajas 2018). Direction of tow (upstream or downstream) is determined based on net flow direction, as EDSM protocol dictates that each tow is conducted against flow. Therefore, tow direction acts as a proxy for tide, where tow is conducted facing downstream during flood tide and upstream

during ebb tide (USFWS, Johnston, et al. 2020). However, note that there may be cases when strong outflow or high water export levels mute tidal effects in certain parts of the estuary. Tide may change at a given site while EDSM conducts their replicate tows, and Delta Smelt may be more easily detected by trawl during flood tide (Bennett and Burau 2015). We also tested the continuous variable cohort day (number of days since July 1) in the detection probability sub-model, because both species are largely annual and will be less abundant over time until the next spawning season. Cohort day was treated the same for both Wakasagi and Delta Smelt based on the otolith data analyzed in this study and Moyle (2002), which indicate both species generally spawn in the springtime within the estuary.

For the occupancy portion of the model, we tested similar covariates to those of the detection probability sub-model: cohort year, region (Figure A2), and cohort day. In addition to these variables, we used water quality information collected at each tow conducted by EDSM, averaged to each site: Secchi depth, conductivity (in $\mu s \times cm^{-1}$, surrogate for salinity), temperature (originally measured in $°C$). Water-quality variables reflect local environmental conditions while region accounts for additional unquantified habitat characteristics (e.g., aquatic vegetation, prey availability, predator abundance, etc.). We assumed these characteristics were static over the modeling time-frame but included cohort year and cohort day to reflect temporal changes in abundance that may affect region occupancy. In particular, cohort year reflects interannual changes in abundance based on recruitment success (and immigration into the estuary in the case of Wakasagi), while cohort day accounts for decreasing abundance between spawning seasons.

For tows with missing water-quality data, we inserted the mean value of that water quality parameter from all samples taken that week within that sub-region (Figure A2). To remove collinearity between cohort day and temperature, we adjusted temperature by cohort day through fitting an ordinary least squares (OLS) regression

with a cubic function ("lm" function) in the R programming environment (R Core Team 2020). Deviance from daily temperature as predicted by the cubic OLS regression model (adjusted $R^2 = 0.94$) was then subsequently used in the occupancy model. All continuous water-quality variables (Secchi depth, conductivity, relative temperature) were z-score-transformed before running the occupancy model, and the quadratic terms for each of these variables were also tested in the model selection.

We used a stepwise forward model selection process to construct a final model for each species. First, the null model and all models with a single variable in either the occupancy or detection sub-model were ranked by Akaike's information criterion adjusted for sample size (AICc). We used lowest AICc as our model selection criterion at the end of each step in the stepwise process. All remaining combinations of a second variable were then added to the lowest-AICc single-covariate model (assuming that the null model did not have the lowest AICc), and all models that had been run at that point were ranked by AICc. This process continued until all possible additional terms had failed to gain lower AICc values relative to models that were run the previous round. Occupancy models were constructed in the R programming environment using the "occu" function in the "unmarked" R package (Fiske and Chandler 2011), and the "aictab" function in the "AICcmodavg" R package (Mazerolle 2019) was used to calculate the AICc value for each model. Intercepts (i.e., reference value) for categorical dummy variables were 2016 for cohort year, North region for region, and Downstream for tow direction.

Growth and Phenology

Otolith-based tools were used to contrast patterns in phenology and growth between Wakasagi and Delta Smelt collected by the YBFMP and rotary screw trap in 2012-2016 (IEP et al. 2019). A total of 130 genetically confirmed Wakasagi (n = 74) and Delta Smelt (n = 56) based on 24 single nucleotide polymorphism (SNP) assays per Benjamin et al. (2018) were selected for analysis (Table 2). Otoliths were processed and analyzed following

Table 2 Wakasagi and Delta Smelt from the Yolo Bypass rotary screw trap used in otolith-based growth and phenology analyses. Sample size (N), fish fork length (FL) and fish age in days post hatch (Age) by year and species

Species	Cohort	N	FL	Age
Wakasagi	2012	17	35.8 (2.8)	66.2 (9.0)
	2013	16	37.0 (4.6)	68.3 (11.2)
	2014	5	35.0 (2.2)	73.1 (8.4)
	2015	4	33.2 (2.2)	76.1 (12.3)
	2016	21	36.1 (4.4)	68.2 (9.7)
Delta Smelt	2012	5	40.8 (3.8)	77.1 (8.5)
	2013	13	38.6 (5.8)	78.7 (11.2)
	2014	3	39.7 (3.5)	80.3 (10.4)
	2015	29	35.9 (5.0)	73.4 (8.4)
	2016	6	38.0 (2.8)	73.4 (8.4)

established protocols (Hobbs et al. 2007; Hobbs et al. 2019; Xieu et al. 2021). In short, sagittal otoliths were dissected from the cranium of each fish using Dupont® SE140 ultra-fine forceps and stored dry in tissue culture trays. Before mounting, otoliths were cleaned by soaking in 95% ethanol for up to 24 hours and any adherent tissue was removed. Cleaned otoliths were then mounted onto glass slides with Crystal Bond® thermoplastic resin in the sagittal plane, sanded to the core on both sides using 1,200 grit wet-dry sandpaper, polished with 0.3-micron alumina on a polishing cloth attached to an MIT polishing wheel (MIT Corp), and finally rinsed with deionized water. Polished otoliths were digitized at 200x magnification using a 12-Megapixel AM Scope digital camera affixed to an Olympus CH30 compound microscope. Multiple images were merged into a composite image using Adobe Photoshop (version 21.1.1). An aging transect was then drawn from the primordium to the dorsal edge at approximately 90 ° to the rostral-postrostral axis of each otolith.

We calibrated composite images of otolith sections using a stage micrometer, and all increments were counted and measured from the hatch check to the dorsal edge using Image-J 4.0 (United States National Institutes of Health; *https://imagej.nih.gov/ij/*). Otolith

increment profiles were quantified by at least two independent analysts, and precision was assessed using the average coefficient of variation (ACV) (Welch et al. 1993; Herbst and Marsden 2011). We included only otoliths with clearly observable rings and repeatable profiles in final anayses, with acceptable consensus defined as an ACV < 10% (Hobbs et al. 2019). If consensus was not achieved across all age readings, the furthest outlier from the mean was discarded, and ACV was recalculated until consensus was achieved or the sample was removed from the analysis. We calculated hatch dates (in the format "year-day") by subtracting each fish's age (number of increments) from its collection date. We calculated total growth rates (mm d^{-1}) by dividing fork length at capture by the otolith-derived age for each fish. Differences among species in phenology and growth were contrasted using linear models. Hatch dates were modeled as the main and interactive effects of species and cohort year. To examine variation in growth, fork length was modeled as a function of daily age (covariate) and the fixed effects of species and cohort year.

Diets

We also examined genetically confirmed Wakasagi and Delta Smelt collected at the Yolo Bypass rotary screw trap for growth and phenology for diet composition. We processed gut samples from fish as described in Mahardja et al. (2019). Food matter that was too digested to be identified to any taxon was categorized under "unidentified." We removed fish that had empty, damaged, or desiccated stomachs from further analysis. In total, 70 Wakasagi (25–58 mm FL) and 38 Delta Smelt (27–50 mm FL) collected between 2010 and 2016 were available for analysis. We compared diet overlap between the two osmerid species by calculating each fish species' index of relative importance (IRI) and conducting a Permutational Multivariate Analysis of Variance (PERMANOVA) analysis. IRI was calculated by summarizing the prey taxon's total frequency of occurrence, percent by count, and percent by weight for each fish species (Chipps and Garvey 2007). We conducted a PERMANOVA test on prey taxon's percent by weight data to assess the differences in diet between the fish species

(Anderson 2001). The PERMANOVA test was run using the "adonis2" function in the "vegan" R package with pairwise Bray–Curtis dissimilarity matrix, 9,999 permutations, and α of 0.05 (R Core Team 2018; Oksanen et al. 2019).

RESULTS

Distribution and Catch Summaries

To determine if Wakasagi abundance or spatial extent is increasing in the estuary, we summarized catch data from trawls, beach seines, screw traps, and salvage. Mean Wakasagi size (mm FL ± SD) from survey types were 15.4 ± 7.8 (larval trawls, n = 1,819), 60.1 ± 14.7; (rotary screw traps, n = 50,419), 49.0 ± 13.7 (beach seines, n = 3,321), and 70.9 ± 22.5 (non-larval trawls n = 2,284) and described in Figure 2.

We gathered data from a total of 11 trawl surveys for sub-adult and adult fishes and 8 trawl surveys for larval or early juvenile fishes to assess catch and range of different life-history stages of Wakasagi (and Delta Smelt for comparative analyses) in pelagic habitat (Table 1, Figure 1). Aside from one Wakasagi in the Bay Study midwater trawl in 1982, Wakasagi catch in Bay-Delta surveys started in 1994. Since this time, larval and juvenile Wakasagi have been caught in several trawls within the Delta demonstrating reproduction within the Delta system (Figure A3). These trawls include the CDFW 20mm survey (n_{max}/yr = 96), Suisun Marsh larval sled (n_{max}/yr = 50), North Bay Aqueduct survey (n_{max}/yr = 100) and Smelt Larva Survey (n_{max}/yr = 273) (Table 1, Figure A3, panel B). Likewise, a reasonably high number of juvenile and adult Wakasagi were caught in the Sacramento Kodiak trawl (n_{max}/yr = 104) and EDSM Kodiak trawl (n_{max}/yr = 859; Figure A4, panel B), with most of the catch from these surveys in the North Delta (the lower Sacramento River from its mouth at the confluence with the San Joaquin River and north to its confluence with the Feather River, Cache Slough, and the SDWSC, and, to a lesser extent, the West and Central Delta around Suisun Bay (Table 1, Figures A4, panel B, and A5). These regional trends are also consistent among other surveys. The Summer Townet survey and Fall
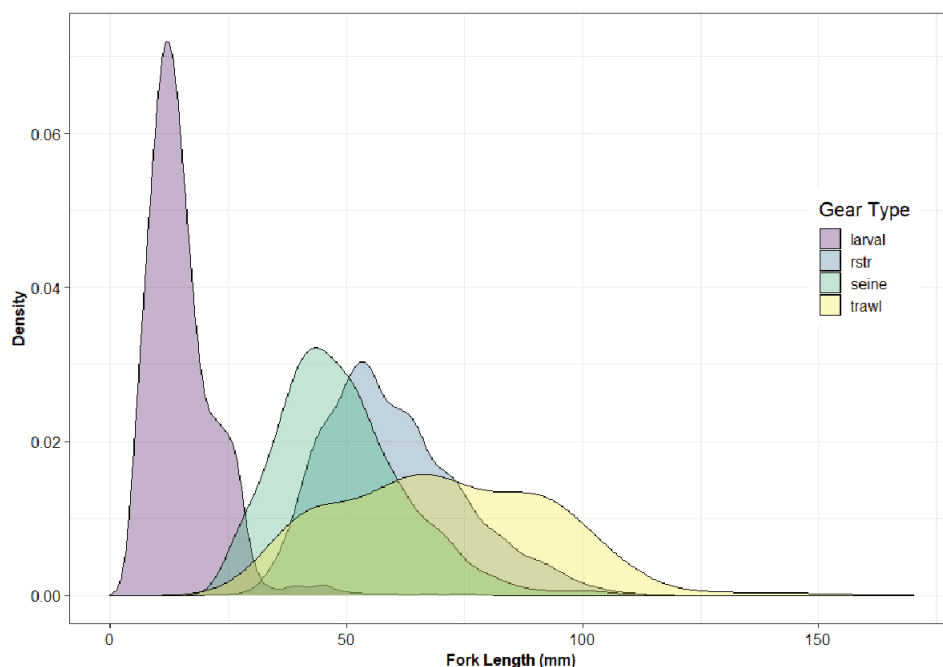
Figure 2   Density plot showing frequency of Wakasagi fork length in millimeters for different gear types: larval trawls (larval), rotary screw traps (rstr), beach seines (seine), and non-larval trawls (trawl)

Midwater Trawl (Table 1), and beach seine data from the DJFMP (Table 1, Figure A6), found most Wakasagi catch in the North Delta, while the Suisun Marsh and Yolo Bypass beach seines recorded low numbers of Wakasagi over the years (n_{total} = 11 and n_{total} = 32 (Figure A7), respectively).

We evaluated data from six rotary screw traps from river channel habitat connecting with the Delta, and one trap in the main channel of the Yolo Bypass within the Delta. We found that a majority of Wakasagi caught are from the Feather River (n_{total} = 249,980, n_{max}/yr = 110,666) or the American River (n_{total} = 6431, n_{max}/yr = 2723), with much lower catch at the Yolo Bypass and Knight's Landing screw traps (Table 1, Figure A8). Abundance in the Sacramento River upstream of Knights Landing was not evaluated, but our results indicate that reservoirs in this region may have lower populations of Wakasagi, or that survival in upstream reaches of the Sacramento River may be poorer. Screw traps on the lower Stanislaus River, which empties into the San Joaquin River and ultimately the South Delta, have not caught Wakasagi in the entirety of their operations. Likewise, Wakasagi are nearly

absent from screw trap catch on the lower Yuba River, which empties into the lower Feather River (downstream from screw trap sites on that river). These data suggest that the Feather River (via Oroville reservoir) and the American River (via Folsom reservoir) are the primary sources for Wakasagi entering the Delta from upstream habitat.

We compared regional (Figure 1A) catch data for Wakasagi and Delta Smelt from four long-term CDFW trawl surveys that are known to catch all life-stages of Delta Smelt (e.g., FMWT, 20-mm trawl, SKT and STN; Tempel et al. 2021). Delta Smelt and Wakasagi catch overlap both spatially and temporally within the north and west Delta and the SDWSC. In absolute terms, Delta Smelt generally comprise a significantly larger proportion of total fish catch than Wakasagi in all four surveys (see Figure 3, specifically for the differences in scale for catch). However, Delta Smelt decline in these surveys is notable, even with the addition of sampling in the SDWSC, where declines within the last 10 years are apparent. At the same time, adult Wakasagi show consistent trends in abundance within the SDWSC

(Figures 3B and 3D). Although it is less clear whether larval and juvenile Wakasagi in the ship channel are increasing or decreasing in relative abundance, their relatively persistent presence there is notable.

Comparative Life-History Traits
Occupancy Model

A total set of 12,211 unique tows make up the EDSM data set used in our occupancy model. In this data set, 1,124 tows were conducted during the 2016 cohort year (phase 1 only), 3,404 tows in the 2017 cohort year (phase 1 and 3), 4,788 tows in the 2018 cohort year (phase 1 and 3), and 2,895 tows in the 2019 cohort year (phase 3 only). Seven Wakasagi were caught in the 2016 cohort year, 257 in 2017, 276 in 2018, and 839 in 2019. In total, Wakasagi were observed in 377 out of 12,211 tows (~3%). In the EDSM data set, 1,183 Wakasagi were caught in the North region, 192 were caught in the West, and 4 were caught in the South (Figure A2). A total of 127 Delta Smelt were caught in the 2016 cohort year, 368 in 2017, 187 in 2018, and 130 in 2019. Delta Smelt were observed in 343 out of 12,211 tows (~2.8%) and the species has been found at least once in every region and cohort year, except for the south region in cohort year 2019.

Our forward model selection approach by AICc resulted in a Wakasagi model with four occupancy variables (with quadratic terms for Secchi depth and temperature) and two detection variables (Table 3; see Table A2 for complete summary of Wakasagi models). Based on this model, Wakasagi occurrence is predicted to decrease with increasing Secchi depth and cohort day (Figure 4). Wakasagi occurrence also appears to be more common where temperature is slightly lower than predicted based on the day of year. Occurrence of Wakasagi is predicted to be highest in the North region (Table 3A). Detection probability for Wakasagi is predicted to decline with cohort day and is highest in the North region, followed by the West region. The wide 95% confidence intervals for the South region in both sub-models (Figure 4) are likely due to the low catch of Wakasagi in this region.

The final model identified for Delta Smelt contains four occupancy variables (with a quadratic term for conductivity) and three detection variables (Table 3; see also Table A3 for complete summary of Delta Smelt models). According to the model, Delta Smelt occupancy decreased between the 2016 and 2019 cohort years and is generally predicted to decline with increasing Secchi depth and conductivity (Figure 5). During the time-period considered here, occupancy was highest in the north region, second highest in the west region, and lowest in the south region. As with Wakasagi, detection probability for Delta Smelt is expected to decrease by cohort day. There is also a potential downward trend in detection probability for Delta Smelt across cohort years. Unlike Wakasagi, Delta Smelt detection probability seems to differ based on whether the tow was conducted downstream or upstream. Towing downstream during flood tide is predicted to have higher detection probability for Delta Smelt compared to towing upstream during ebb tide.

Growth and Phenology

The mean ± s.d. sizes (mm fork length, FL) of Delta Smelt and Wakasagi used in otolith analyses were 37.3 ± 5.0 mm and 36.0 ± 3.8 mm, respectively (Table 2). Mean ± s.d. ages (days-post-hatch, dph) of each species were 75.5 ± 9.2 and 68.9 ± 10.4 dph, respectively. Total growth rates of Wakasagi and Delta Smelt ranged from 0.4 to 0.7 mm d^{-1} and did not differ significantly between species (Figure 6A–6E, Table 4). Growth for both species did, however, differ among years, with the lowest growth rates observed during extreme drought in 2014–2015.

Phenology (hatch dates) varied significantly among species, with Wakasagi hatching approximately 1 month earlier than Delta Smelt in most years (Figure 6F–6J, Table 4). Hatch dates also varied among years, occurring earliest for both species in 2015 during an extremely warm drought period. No significant interaction between species and year was observed; however, the overlap in hatch dates observed in 2012, a cooler year, was indicative of potential temporal variation in relative hatch dates, particularly for
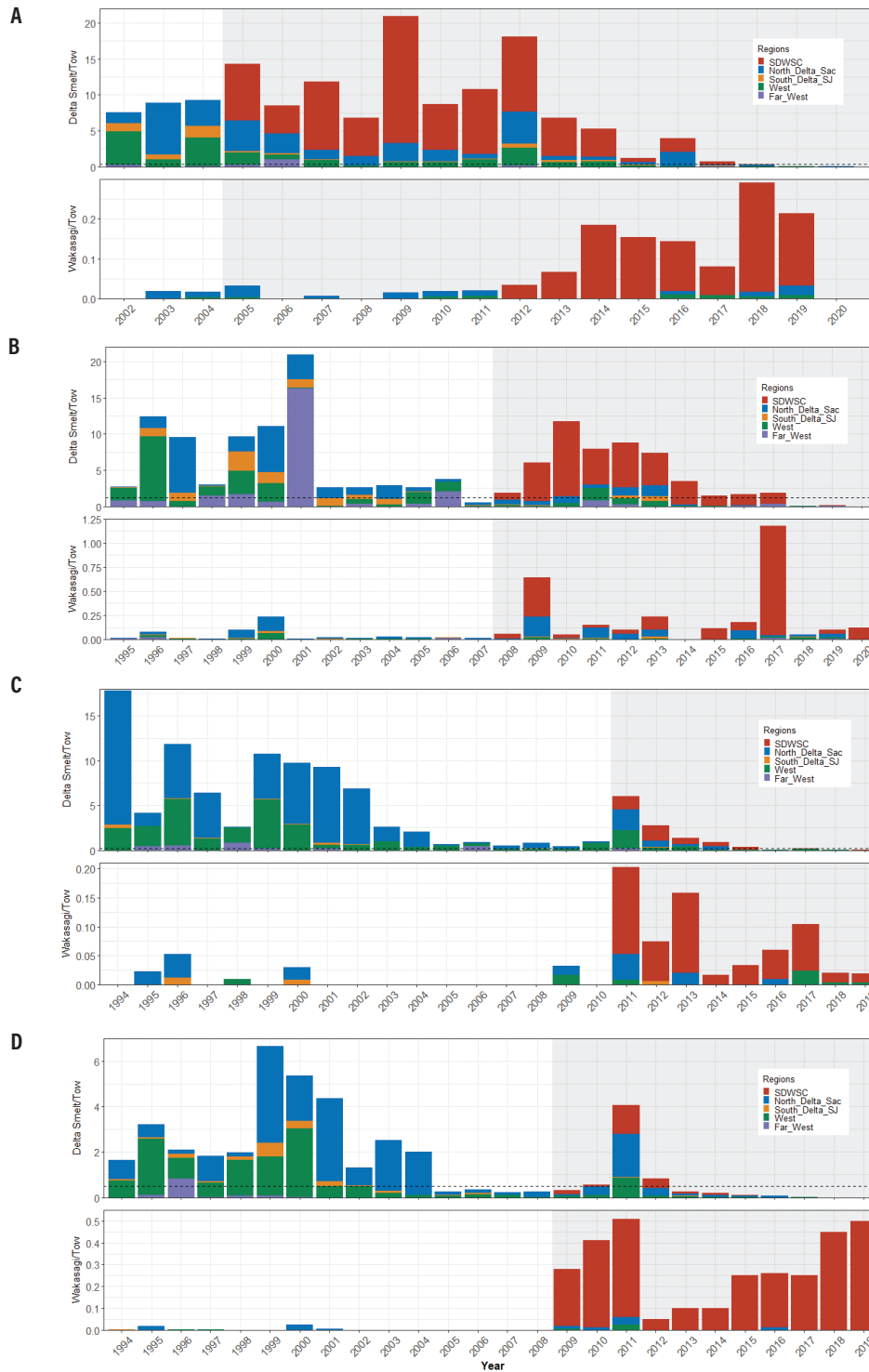
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Figure 3 Delta Smelt and Wakasagi annual mean catch per tow for Bay-Delta regions (Figure 1A). (**A**) Spring Kodiak Trawl (Jan–May, adults); (**B**) 20-mm survey (Mar–Jul, post-larval-juvenile); (**C**) Summer Townet survey (Jun–Aug, juvenile–sub-adult); (**D**) Fall Midwater Trawl (Sep–Dec, sub-adult–adult); note different X-axes. *Grey shading* shows start of sampling in the Sacramento Deepwater Ship Channel (SDWSC) for each survey. For visual comparison of abundance between species in a given survey, the top of the Y-axis scale for Wakasagi catch per tow is shown as a *dotted line* on the Delta Smelt panel for the same survey.

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Table 3 Model parameter estimates for the final (**A**) Wakasagi and (**B**) Delta Smelt occupancy models. Reference levels for categorical variables Region and Cohort Year are North and 2016, respectively, for Wakasagi; reference levels for categorical variables Region, Cohort Year, and Tow Direction are North, 2016, and Downstream, respectively, for Delta Smelt. Values shown for continuous variables are based on z-standardized data.

A. WAKASAGI						
	Variable	**Categorical level**	**Estimate**	**SE**	**z**	**P(>|z|)**
Occupancy	Intercept		− 2.109	0.248	− 8.508	< 0.001
	Secchi depth		− 2.765	0.197	− 14.059	< 0.001
	Secchi depth2		1.128	0.179	6.312	< 0.001
	Region	South	− 0.677	1.816	− 0.373	0.709
		West	− 2.220	0.268	− 8.292	< 0.001
	Cohort Day		− 0.014	0.002	− 7.099	< 0.001
	Temperature		− 0.482	0.115	− 4.173	< 0.001
	Temperature2		− 0.194	0.083	− 2.351	0.019
Detection	Intercept		1.084	0.212	5.120	< 0.001
	Region	South	− 2.801	1.975	− 1.418	0.156
		West	− 1.412	0.230	− 6.135	< 0.001
	Cohort Day		− 0.008	0.002	− 4.088	< 0.001
B. DELTA SMELT						
	Variable	**Categorical level**	**Estimate**	**SE**	**z**	**P(>|z|)**
Occupancy	Intercept		1.546	0.905	1.708	0.088
	Secchi depth		− 3.436	0.365	− 9.420	< 0.001
	Region	South	− 2.792	0.657	− 4.251	< 0.001
		West	− 1.694	0.428	− 3.963	< 0.001
	Conductivity		− 0.047	0.328	− 0.142	0.887
	Conductivity2		− 0.242	0.151	− 1.596	0.110
	Cohort Year	2017	− 2.094	0.852	− 2.457	0.014
		2018	− 3.994	0.871	− 4.588	< 0.001
		2019	− 4.082	0.914	− 4.467	< 0.001
Detection	Intercept		1.604	0.307	5.218	< 0.001
	Cohort Day		− 0.016	0.001	− 13.609	< 0.001
	Cohort Year	2017	− 1.402	0.263	− 5.335	< 0.001
		2018	− 0.615	0.234	− 2.625	0.009
		2019	− 1.904	0.402	− 4.741	< 0.001
	Tow Direction	Upstream	− 0.437	0.142	− 3.070	0.002

Wakasagi. Distributions of hatch dates by species and year, and size at age and daily growth based on otolith increment profiles, are provided in Figures A10 and A11.

Diets

Twenty-nine prey items were identified in Wakasagi and 11 items in Delta Smelt diets that were collected from the Yolo Bypass Toe Drain; however, diet composition for Wakasagi and Delta Smelt (Table 5) were largely the same. The calanoid copepod *Pseudodiaptomus forbesi* was the most dominant prey item consumed by Wakasagi, making up 78.5% of total prey item count, 99.2% of total weight, and present in 94.3% of analyzed Wakasagi (Table 5A). Similarly, *P. forbesi* was the primary prey item consumed by Delta Smelt in terms of numbers (84.8% of total prey item count), weight (74.8% of total weight), and frequency of occurrence (94.7% of analyzed fish) (Table 5B). *P. forbesi* made up the highest proportion of IRI for both Delta Smelt and Wakasagi, with little
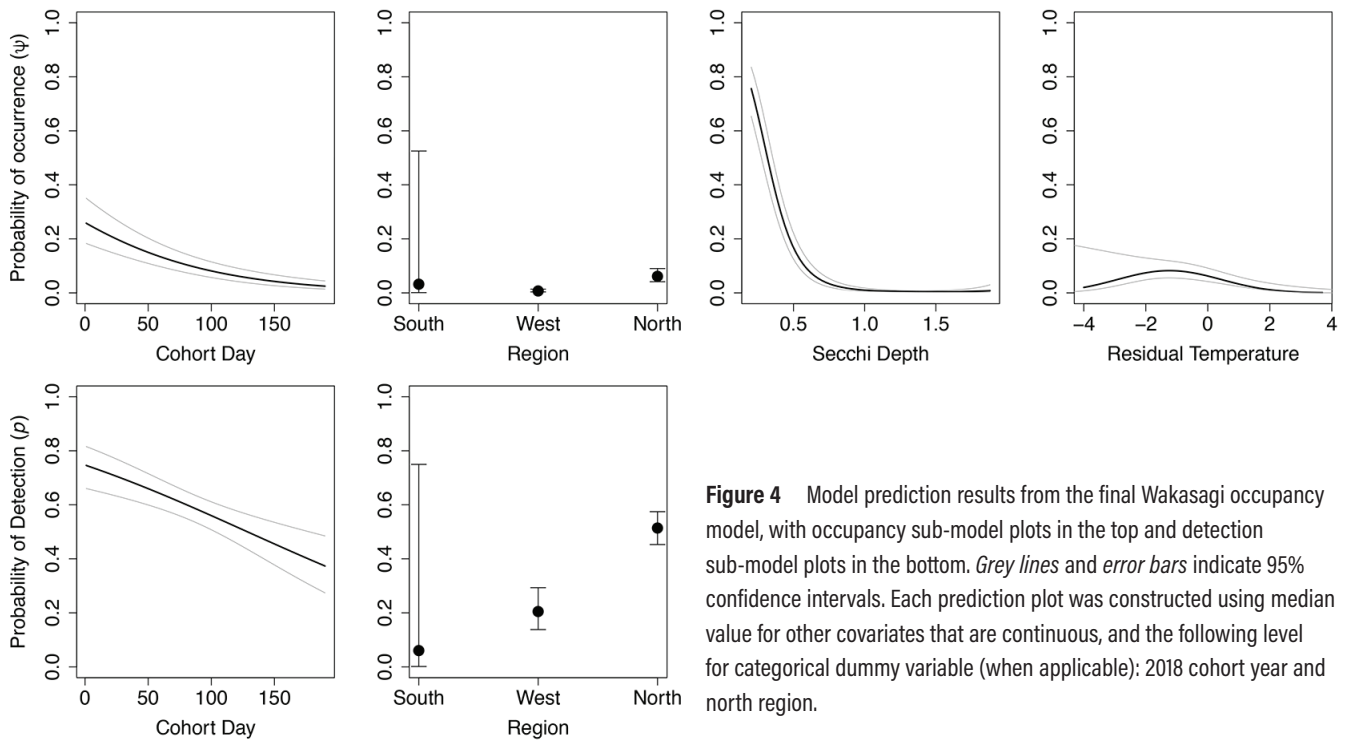
Figure 4   Model prediction results from the final Wakasagi occupancy model, with occupancy sub-model plots in the top and detection sub-model plots in the bottom. *Grey lines* and *error bars* indicate 95% confidence intervals. Each prediction plot was constructed using median value for other covariates that are continuous, and the following level for categorical dummy variable (when applicable): 2018 cohort year and north region.
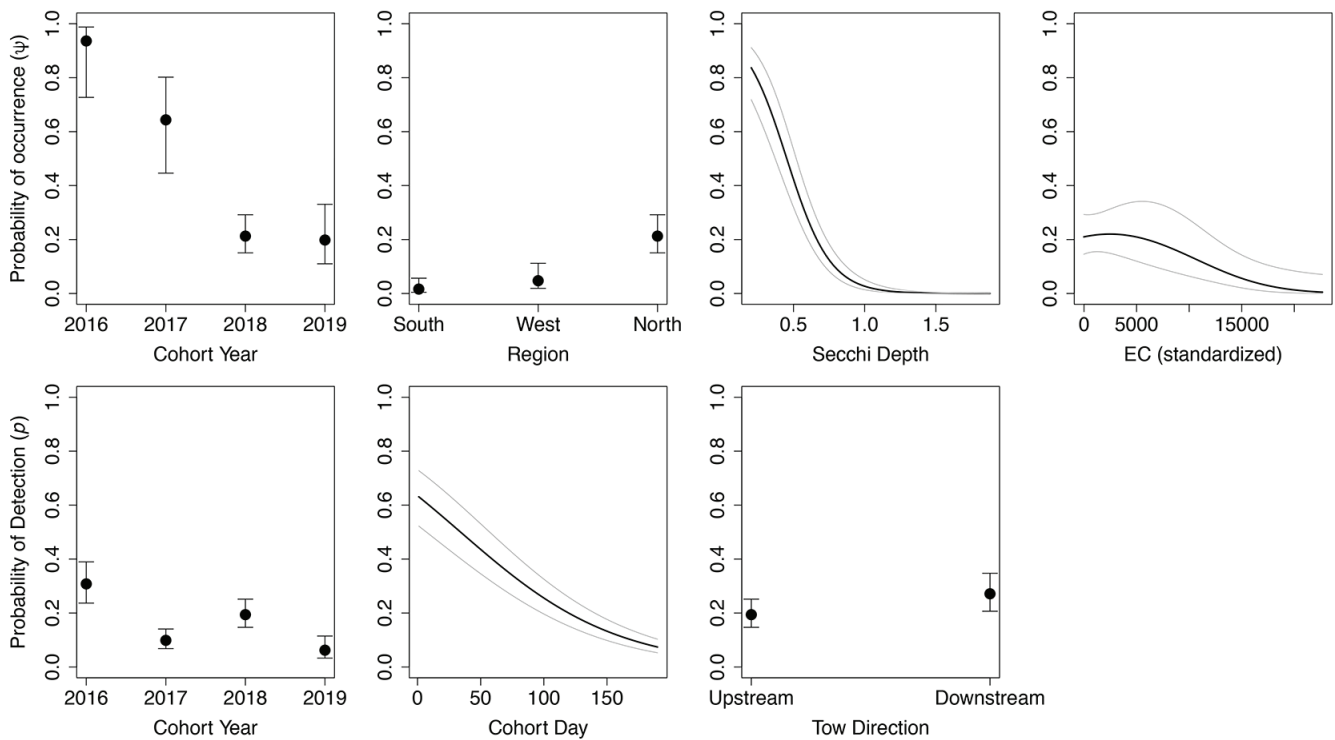
Figure 5   Model prediction results from the final Delta Smelt occupancy model, with occupancy sub-model plots in the top and detection sub-model plots in the bottom. *Grey lines* and *error bars* indicate 95% confidence intervals. Each prediction plot was constructed using median value for other covariates that are continuous, and the following level for categorical dummy variable (when applicable): 2018 cohort year and north region.
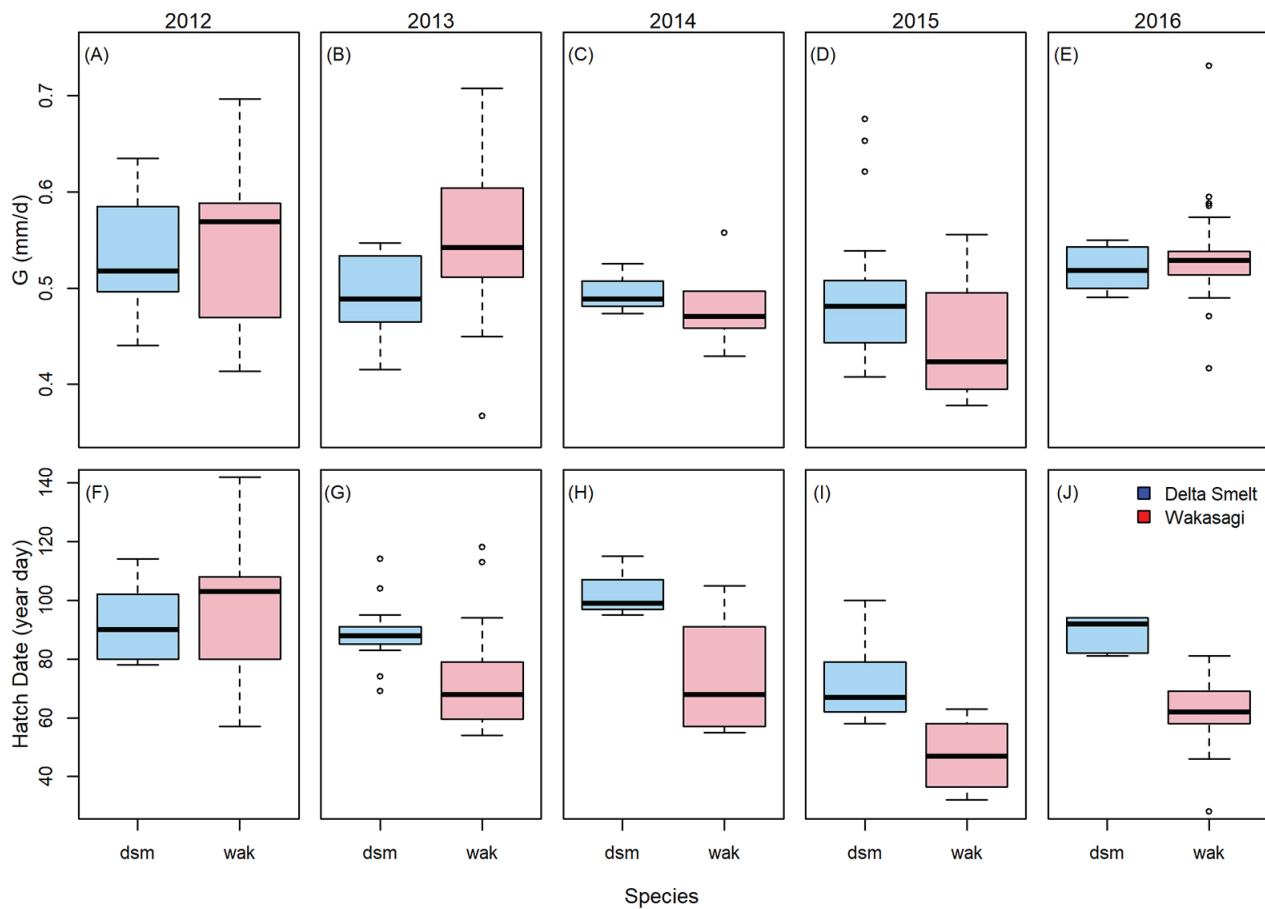
Figure 6 Variation in growth rates (**A–E**) and hatch dates (**F–J**) between species (Delta Smelt: dsm, Wakasagi: wak) and among years (2012–2016)

Table 4 Results of linear models examining differences in phenology and growth between Wakasagi and Delta Smelt

Metric	Factor	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig	adjR²
Phenology (hatch date)	Species	1	1385.6	1385.6	5.8676	0.017	*	0.42
	Year	5	19064	3812.8	16.1458	< 0.001	***	
	Species x Year	5	2649.2	529.8	2.2436	0.055	.	
	Residuals	109	25740.2	236.1				
Growth (fork length)	Age	1	558.25	558.25	39.9385	< 0.001	***	0.30
	Species	1	0.01	0.01	0.0004	0.984		
	Year	5	247.22	49.44	3.5374	0.005	**	
	Residuals	113	1579.48	13.98				

*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

contribution from other prey species (Table 5, Figure A12). *Sinocalanus doerrii*, another calanoid copepod species, had the second highest IRI for the two osmerid fish species, with slightly larger proportion of IRI seen in Delta Smelt as compared to Wakasagi (Table 5). A PERMANOVA test to assess difference in diet between Delta Smelt and Wakasagi was not significant (R^2 = 0.008, p = 0.55).

DISCUSSION

In this study, we provide valuable analysis to improve the information available for the ecology and life-history of Wakasagi, a non-native fish in the estuary and congener to the critically endangered Delta Smelt. Unlike many other non-native fish species that have been introduced into the estuary and rapidly increased in abundance and distribution (Dill and Cordone 1997), we found Wakasagi abundance to be relatively limited. Within the scope of the monitoring surveys we investigated, Wakasagi were detected throughout the estuary, though persisted in greatest abundance only within the northern region of the estuary. Comparatively, we found similarities (or overlap) in the ecology and life-history between these Wakasagi and Delta Smelt as demonstrated by the somewhat similar habitat associations, growth, diets, and phenology. We did find subtle shifts in phenology of Wakasagi to cooler temperatures demonstrated by hatch dates, indicating they may exhibit similar sensitivity to environmental variability as Delta Smelt. This study provides an example of how synthesis studies linking long-term field data and laboratory data can better inform species conservation and management. For example, if we had only evaluated one or two life-history traits (e.g., diet, occupancy model) we might have concluded Wakasagi had a significant negative effect on Delta Smelt based on their similarities in traits. However, the limited abundance and patchy distribution of Wakasagi in the estuary despite relatively large numbers upstream suggest that severe negative interactions with Delta Smelt have been limited or infrequent.

Distribution, Abundance, and Occupancy

Our initial study goal was to better describe the status of the Wakasagi population in the estuary by determining if the population has expanded spatially and in abundance. Collectively, analysis of fish surveys demonstrated that Wakasagi have expanded their range throughout the Central Valley since their initial introduction in 1959 (Dill and Cordone 1997; Moyle 2002) and continue to be abundant in some reservoirs and tributaries. Yet, Wakasagi abundance has remained relatively low in the estuary over the past several decades compared to Delta Smelt, and Wakasagi are primarily found in the northern Delta where the species co-occur (Figure 3). Because of the morphological similarities between Wakasagi and Delta Smelt (Fisch et al. 2014, Benjamin et al. 2018), it is unclear how much we can gather from the estuarine catch patterns from earlier years (~ pre-2010) when Wakasagi catches were sporadic and species identification was less consistent (Kirsch et al. 2018); however, the large patterns evident from our data are highly unlikely to be driven solely by species misidentification. In particular, all Wakasagi captured by the DJFMP and EDSM have been returned to the office for further confirmation on their species identification since 2017, and Delta Smelt are regularly retained for various analyses, thereby reducing the probability of misidentification over the time-frame of the occupancy model. Based on the rotary screw trap data (Figure A8), Wakasagi should move downstream into the Delta at relatively high numbers throughout most years from the Feather River, American River, and the mainstem Sacramento River. This transport would explain Wakasagi's higher occurrence in the northern Delta relative to elsewhere in the estuary, but Wakasagi have overall been less common in the estuary than the rare and endangered Delta Smelt (until recently, see below). However, it should be noted that sampling effort does vary between the mainstem Sacramento and San Joaquin rivers, and Wakasagi production does occur in the estuary as evidenced by larval surveys (Figures A3, A4), and may alternatively explain increased occurrence in the northern Delta.

Table 5 Summary of diet composition information from (**A**) Wakasagi and (**B**) Delta Smelt collected in the Yolo Bypass Toe Drain (N = 70 and N = 38 for Wakasagi and Delta Smelt, respectively). %N is percent of total by count, %W is percent of total by weight, %FO is frequency of occurrence, and %IRI is percentage of Index of Relative Importance (IRI) for the fish species.

A. WAKASAGI

Prey item	Total count	Total weight (g)	%N	%W	%FO	%IRI
Pseudodiaptomus forbesi	3,567	2.056	78.516	99.214	94.286	97.406
Sinocalanus doerrii	168	0.003	3.698	0.159	50.000	1.121
Calanoida	164	0.002	3.610	0.082	17.143	0.368
Unidentified	27	0.007	0.594	0.328	38.571	0.207
Cyclopoida	118	0.001	2.597	0.034	12.857	0.197
Acanthocyclops spp.	107	0.001	2.355	0.034	12.857	0.179
Bosmina longirostris	120	0.000	2.641	0.000	11.429	0.175
Daphniidae	57	0.000	1.255	0.010	22.857	0.168
Ceriodaphnia spp.	40	0.001	0.880	0.024	11.429	0.060
Daphnia spp.	42	0.001	0.924	0.039	10.000	0.056
Moina spp.	47	0.001	1.035	0.029	2.857	0.018
Diaptomidae	14	0.000	0.308	0.010	7.143	0.013
Harpacticoida	10	0.000	0.220	0.000	8.571	0.011
Diacyclops spp.	11	0.000	0.242	0.000	4.286	0.006
Eurytemora affinis	11	0.000	0.242	0.000	4.286	0.006
Alona spp.	12	0.000	0.264	0.000	1.429	0.002
Gastropoda	5	0.000	0.110	0.000	2.857	0.002
Osteichthyes	3	0.001	0.066	0.024	2.857	0.001
Copepoda	7	0.000	0.154	0.000	1.429	0.001
Chydorus spp.	3	0.000	0.066	0.000	2.857	0.001
Chydoridae	2	0.000	0.044	0.000	1.429	0.000
Americorophium stimpsoni	1	0.000	0.022	0.014	1.429	0.000
Bivalvia	1	0.000	0.022	0.000	1.429	0.000
Chironomidae	1	0.000	0.022	0.000	1.429	0.000
Corophiidae	1	0.000	0.022	0.000	1.429	0.000
Eucyclops spp.	1	0.000	0.022	0.000	1.429	0.000
Laophontidae	1	0.000	0.022	0.000	1.429	0.000
Ostracoda	1	0.000	0.022	0.000	1.429	0.000
Plant matter	1	0.000	0.022	0.000	1.429	0.000

B. DELTA SMELT

Prey item	Total count	Total weight (g)	%N	%W	%FO	%IRI
Pseudodiaptomus forbesi	1,230	0.018	84.828	74.797	94.737	91.829
Sinocalanus doerrii	126	0.003	8.690	12.195	52.632	6.675
Unidentified	7	0.002	0.483	9.350	18.421	1.100
Acanthocyclops spp.	40	0.000	2.759	1.220	7.895	0.191
Diaptomidae	15	0.000	1.034	1.626	5.263	0.085
Ceriodaphnia spp.	10	0.000	0.690	0.000	13.158	0.055
Daphnia spp.	4	0.000	0.276	0.407	5.263	0.022
Cyclopoida	9	0.000	0.621	0.000	5.263	0.020
Daphniidae	4	0.000	0.276	0.000	5.263	0.009
Calanoida	2	0.000	0.138	0.407	2.632	0.009
Diacyclops spp.	3	0.000	0.207	0.000	5.263	0.007

Catch of Wakasagi outside of the northern Delta is possible but seems to be mostly ephemeral (see Figures A3–A5, A9). Environmental conditions in the interior Delta seem unsuitable for Wakasagi, with low detections in the Mossdale trawl and the species' absence from some San Joaquin River tributaries (Table 1), indicating that their expansion and/or proliferation into the San Joaquin River system to the south is likely limited. Similar to Delta Smelt, Wakasagi have been detected at state and federal salvage facilities (Figure A9) in the South Delta since 1995, but these Wakasagi likely came from the Central and North Delta and less from the San Joaquin River or tributaries, as indicated by rare detections there. Wakasagi detections in salvage monitoring are likely to be highly under-representative of the overall level of entrainment because of low estimated survival rates prior to the salvage facilities, as seen in Delta Smelt (Castillo et al. 2012). However, we were not able to evaluate all tributaries for transport of Wakasagi from reservoirs to the San Joaquin River, or assess local reproduction in the lower San Joaquin River, though some larvae are caught in the southern estuary (Figure A3). There is also speculation of Wakasagi presence in the San Luis reservoir being from individuals transported by the California Aqueduct (Hess et al. 1995; Aasen et al. 1998); however, it is unclear if Wakasagi are well established in the reservoir or if they could survive in other southern California reservoirs via transported water.

A secondary goal of our study was to evaluate if Wakasagi demonstrate similar ecological traits as native congener Delta Smelt. Our occupancy model results indicate that Wakasagi and Delta Smelt share a common association with high turbidity but differ in terms of other physical habitat associations. Our finding that Delta Smelt occupancy is higher at lower conductivity (lower salinity) is consistent with the general description of Delta Smelt as an estuarine species with limited salinity tolerance (Bennett 2005). Although Wakasagi can tolerate wider ranges of salinity and temperature than Delta Smelt (Swanson et al. 2000), our results may reflect a Wakasagi preference for cooler temperatures. For the

time-frame modeled here, patterns in Wakasagi occupancy and detection were driven more by regional and within-cohort year effects, while Delta Smelt patterns were driven by between-cohort year effects with an overall decreasing trend. Furthermore, whereas Delta Smelt were found at various locations between 2016 and 2019 through the recently established intensive EDSM survey, Wakasagi were largely found in the northern and western regions (Figure A2) that correspond to the SDWSC Channel and Suisun Marsh, respectively. The SDWSC and Suisun Marsh have been known as hotspots for Delta Smelt (Polansky et al. 2018) due to the existence of a favorable high turbidity zone and increased food availability (Feyrer et al. 2017; Young et al. 2021). We hypothesize that these characteristics make these areas favorable to Wakasagi as well.

Our occupancy modeling warrants further discussion with regard to model assumptions and interpretation. Because the estuary is a highly dynamic aquatic environment, we do not know the extent to which the site-level closure assumption is satisfied. The delineation of a site depends on the horizontal distance traveled by the boats, the vertical coverage of the trawl within the water column, and the local hydrodynamics. Although replicate tows at a site are conducted close together in time, with an average of 15 minutes between tows, occupancy status can potentially change between tows, depending on hydrodynamics and fish movement. Generally, violations of model assumptions can lead to biased parameters and incorrect inferences about covariate effects. However, if movement of Wakasagi and Delta Smelt in and out of a site can be considered random, the resulting occupancy and detection estimates are not necessarily biased, though their interpretations change (Kendall 1999). In this context, occupancy is now the proportion of sites used by the target species, and detection is the product of the probability that the species was present at the site and the probability that it was detected given that it was present (MacKenzie 2005). We included covariates in the occupancy sub-model to reduce unmodeled heterogeneity, which can inflate occupancy variance estimates (MacKenzie

et al. 2006, p. 106–107). Similarly, we included covariates in the detection sub-model to reduce unmodeled heterogeneity in detection, which often results in negatively biased occupancy estimates and difficulties in determining model structure (MacKenzie et al. 2006, p. 107). This analysis could be extended by considering a larger set of covariates (e.g., food availability) and incorporating local colonization and extinction rates to account for Wakasagi immigration into the estuary from source reservoirs. Nevertheless, occupancy models represent a more robust approach than logistic regression models that assume perfect detection. Moreover, previous studies on Delta Smelt showed results consistent with our study (Polansky et al. 2018), found little evidence for major violations of the closure assumption with temporal replicates similar to our study (Peterson and Barajas 2018), and recommended temporal replicates over spatial replicates for understanding the effects of environmental variables on occupancy (Duarte and Peterson 2021). As such, we believe that the larger patterns we observed in our final occupancy models (e.g., higher occupancy for both species at low Secchi depth and conductivity values, declining detection probability for Delta Smelt over the years, etc.) should generally stand, regardless of the statistical approaches. The limited range and relatively low catch of Wakasagi, despite a continuous supply of fish from upstream reservoirs, differs from the common image of a rapidly expanding invasive population. And while Wakasagi and Delta Smelt exhibit similar niches, Delta Smelt may, in fact, be better adapted to the upper estuary despite all the anthropogenic changes that have occurred to the system. This trend, however, may be reversing with the apparent increase of Wakasagi abundance and corresponding decline of Delta Smelt abundance in recent years (Figure 3). In the record dry year of 2021, we saw yet another year of historically low Delta Smelt numbers while hundreds of Wakasagi were caught in the SDWSC (USFWS et al. 2021). It is important to note, however, that despite the higher number of Wakasagi in 2021, Wakasagi still make up a small portion of the total fish catch relative to the more commonly found non-native species

of the upper estuary (e.g., Largemouth Bass *Micropterus salmoides*, Mississippi Silverside *Menidia audens*, Threadfin Shad *Dorosoma petenense*, etc.), and Wakasagi seem unlikely to play a substantial role in the estuary's food web at the moment. However, Wakasagi may not need to be a substantial part of the food web to have detrimental effects on Delta Smelt through mechanisms such as hybridization (Fisch et al. 2014; Benjamin et al. 2018).

Growth, Phenology, and Diet
Wakasagi and Delta Smelt exhibited similar patterns in growth and diet in the Yolo Bypass toe drain, further suggesting that this backwater slough environment can support populations of both species. The similarities in growth rates and diets (a proxy for foraging patterns) (Figure 6, Table 5, Figure A10) suggest that these two osmerid species likely serve overlapping ecological roles in the Yolo Bypass, each contributing similarly to pelagic food webs as secondary consumers and yielding similar tertiary production as forage fish. Both species showed diet selectivity, with calanoid copepods comprising 85% and 94% prey count of Wakasagi and Delta Smelt gut contents, respectively. Calanoid species were mainly *Psedodiaptomus forbesi* and *Sinocalanus doerrii* with >95% IRI for both species, consistent with previous Delta Smelt diet studies (Slater and Baxter 2014; Moyle et al. 2016; Mahardja et al. 2019). However, we note that diet data in our study were gathered only from the Yolo Bypass, and Wakasagi may have a more variable diet composition overall, based on a previous study on Delta Smelt diet that demonstrated a more diverse diet than what is shown in our study (Slater and Baxter 2014). Wakasagi from the Yolo Bypass had more than double the prey items as Delta Smelt (Table 5) which may suggest different foraging strategies and potentially a competitive advantage; however, this is uncertain given our analysis of a single habitat within the larger estuary. Regardless, given their similar growth rates and diets in the bypass, earlier hatching by Wakasagi results in larger sizes of recruits on a given calendar date than co-occurring Delta Smelt. During spring–summer, this larger size-at-date

may confer an advantage to Wakasagi, whose advanced development may result in higher foraging success and reduced susceptibility to predators than smaller, newly hatched Delta Smelt. Alternatively, differences in hatch dates may result in interannual patterns in match and mismatch between hatching and prey abundance.

Growth of Wakasagi and Delta Smelt is likely affected by environmental variation, though no study has been done to fully evaluate the environmental drivers of Wakasagi growth rates. We found that total growth rate did not vary among species, but it did differ among years, with the lowest growth rates observed during extreme drought conditions in 2014–2015. A recent study using otolith increment analysis demonstrated that growth rates of wild Delta Smelt are strongly influenced by environmental variation (Lewis et al. 2021). For example, warming temperatures were associated with reduced growth rates, and this effect was intensified when fish were observed in warmer and clearer (i.e., low turbidity) conditions. Given that Wakasagi hatched earlier and reared in cooler waters relative to Delta Smelt, warming conditions may also negatively affect growth rates of larval and juvenile Wakasagi, depending on food availability.

The phenology of Delta Smelt and Wakasagi differed among species and appeared to vary with changes in weather. In most years, Wakasagi hatched approximately 30 days earlier than Delta Smelt, indicating that Wakasagi may require cooler temperatures than Delta Smelt for successful spawning, hatching, or rearing. Hatch dates also varied among years, occurring earliest for both species in 2015 (during an extreme drought period), a year with particularly warm average water temperatures (Bashevkin and Mahardja 2021; 2022 data file from C. Pien, USBR–DWR, to B. Davis, unreferenced, see "Notes"). This result is supported by recent otolith analyses indicating that the phenology of Delta Smelt is highly sensitive to variation in climate. For example, the phenology of Delta Smelt varied significantly with mean winter temperatures, with median hatch dates being 60 days earlier in warmer versus cooler years (Lewis et al. 2022).

Furthermore, relative hatch dates of Wakasagi increased and overlapped with those of Delta Smelt during cooler conditions in 2012. Analysis of water temperature trends from long-term fish monitoring surveys (e.g., calculations of mean, 75% quartile, and maximum temperature at detection [2022 data file from C. Pien, USBR–DWR, to B. Davis, unreferenced, see "Notes"; Bashevkin et al. 2022]) showed Wakasagi larvae were detected at temperatures 2–3 °C cooler than Delta Smelt as compared to more similar temperatures of juveniles and adult detections supporting sensitivity of early-life stages of Wakasagi. Given that Wakasagi hatch earlier and rear in cooler waters relative to Delta Smelt, these results suggest that the phenology of Wakasagi may be even more sensitive to weather and climate variability than that of Delta Smelt.

Based on laboratory studies using wild-caught fish, subadult–adult (40–70 mm) Wakasagi appear to tolerate a wider range of environmental conditions better than Delta Smelt of similar sizes (Swanson et al. 2000). For example, Wakasagi exhibited higher critical thermal maxima, lower critical thermal minima, higher salinity tolerances, and were faster swimmers than Delta Smelt. The authors concluded that conditions in the Delta should not exclude Wakasagi from the system, and that the dynamic nature of the Delta may confer a "physiological disadvantage" for Delta Smelt relative to Wakasagi. Given these results, the authors noted that it remains surprising that Wakasagi exhibit relatively low abundance in the Delta, "although their eggs and larvae may be less tolerant." Our results here demonstrate that Wakasagi can feed and grow similarly to Delta Smelt in a tidal slough within the North Delta. However, we also show that surviving Wakasagi hatched and reared during cooler months and exhibited similar reductions in growth during warmer years, thus suggesting that early life stages may not be as physiologically tolerant to environmental variation as adults.

Management Implications

Many studies in the estuary are focused on threatened and endangered species such salmonids and Delta Smelt; however, these

species of conservation concern do not exist in isolation, and understanding their interaction with other species can provide new insight into their population dynamics and the efficacy of our management actions. Limited resources often mean fewer studies on the various invasive species; however, our study provides a good example of why it is useful to collect information on less abundant species that may indirectly or directly influence species of concern and affect management efforts to conserve them. By demonstrating the similarities of Wakasagi and Delta Smelt in this study, we can use future detections of Wakasagi in the field to inform suitability of habitats for supplementation releases of cultured Delta Smelt, evaluate the growing concern of contaminants, or potentially determine the efficacy of food subsidy actions. Likewise, conditions in the Delta that are currently unfavorable for Delta Smelt may also be contributing to reduced Wakasagi abundances, and efforts to improve habitat for Delta Smelt may also have affect Wakasagi.

With Delta Smelt currently at critically low abundances in the wild, cultured fish held in enclosures in the wild are being used as surrogates to inform the adaptive management of targeted flow actions and restoration projects (Lessard et al. 2018). Plans are in development for population supplementation by conducting releases of cultured Delta Smelt into the wild (USFWS, CDWR, et al. 2020). Results from this study suggest that Wakasagi hatcheries and studies in Japan may provide useful insight for the development of Delta Smelt hatchery practices and studies in the estuary (Kuge 2006; 2021 file from T. Hung, UCD-DWR emailed to BED, unreferenced, see "Notes"). The success of potential supplementation releases will hinge on a multitude of factors not considered here, but another important factor is the degree to which wild Wakasagi (that are more abundant in Delta Smelt habitat today) will interact with cultured Delta Smelt. Our results indicate a high degree of niche overlap between these species, though it is unknown whether cultured Delta Smelt will interact with wild Wakasagi differently than with wild Delta Smelt. Nevertheless, continued

monitoring of habitats that receive supplemented Delta Smelt, with genetic analysis of all collected smelts, will be critical to understanding any potential interactions.

Results presented suggest Wakasagi may be a potential surrogate species for management of Delta Smelt habitat. Together, we found evidence of co-occurrence in range and that these species serve a similar ecological role demonstrated by overlaps in annual spawning and phenology, growth, and food web contributions as secondary consumers and likely tertiary prey. Despite the generally low abundance of Wakasagi in the estuary, future detection of the species at tidal wetland restoration sites may provide vital information on the relative suitability of those areas for Delta Smelt. Overall, similarities and sensitivities of Wakasagi and Delta Smelt suggest that Wakasagi may be of use as a substitute species (Caro et al. 2005) for testing management tools to inform Delta Smelt conservation strategies.

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