California Fish and Game 99(3):122-148; 2013

Longfin smelt: spatial dynamics and ontogeny in the San Francisco Estuary, California

Joseph E. Merz*, Paul S. Bergman, Jenny F. Melgo, and Scott Hamilton

Cramer Fish Sciences, 13300 New Airport Road, Auburn, CA 95602, USA (JEM, JFM, PSB)

Center for California Water Resources Policy and Management, 1017 L Street #474, Sacramento, CA 95814, USA (SH)

**Correspondent: jmerz@fishsciences.net*

We utilized recently available sampling data (~1959-2012) from the Interagency Ecological Program and regional monitoring programs to provide a comprehensive description of the range and temporal and geographic distribution of longfin smelt (*Spirinchus thaleichthys*) by life stage within the San Francisco Estuary, California (Estuary). Within 22 sampling regions, we identified 357,538 survey events at 1,203 monitoring stations. A total of 1,035,183 longfin smelt (LFS) were observed at 643 stations (53%) in an area from Central San Francisco Bay (Tiburon) in the west, to Colusa on the Sacramento (Sacramento Valley region) in the north, Lathrop on the San Joaquin River (border of South Delta and San Joaquin River regions) to the east and South San Francisco Bay (Dumbarton Bridge) to the south, an area of approximately 137,500 ha. We found that LFS were frequently observed across a relatively large portion of their range, including East San Pablo Bay north into Suisun Marsh down through Grizzly Bay and all four regions of Suisun Bay through the Confluence to the Lower Sacramento River region. Unlike juvenile LFS, whose locations fluctuate between the bays and Suisun Marsh in relation to the low salinity zone, adults during the spawning period appeared to be not only in these locations but also in upper Delta reaches and also into San Francisco Bay, likely indicating that LFS spawning habitat may extend further upstream and downstream than LFS rearing habitat. The anadromous life stage declined in spring and mid-summer but increased throughout fall months across all areas, suggesting immigration and emigration through the Estuary. Longfin smelt appeared to migrate completely out of the lower rivers by July but some adults consistently remained in downstream Estuary areas, suggesting not all individuals demonstrate marine migration. This comprehensive data review provides managers and scientists an improved depiction of the spatial and temporal extent of LFS throughout its range within the Estuary and lends itself to future population analysis and restoration planning for this species.

Key words: Longfin smelt, San Francisco Estuary, distribution, *Spirinchus thaleichthys,* spatial analysis, life stage, observed presence

---

The longfin smelt (*Spirinchus thaleichthys*) is a small (i.e., 90–110 mm standard length [SL] at maturity), semelparous, pelagic fish that has been observed in estuaries of the North American Pacific Coast, from Prince William Sound, Alaska to Monterey Bay, California with landlocked populations occurring in Lake Washington, Washington and Harrison Lake, British Columbia (McAllister 1963, Dryfoos 1965, Moulton 1979, Chigbu and Sibley 1994, Chigbu et al. 1998, Chigbu and Sibley 1998, Baxter 1999, Moyle 2002, Rosenfield and Baxter 2007). In California, the longfin smelt inhabits the San Francisco Estuary (Estuary), Humbodlt Bay, and Eel, Klamath and Smith rivers (Baxter 1999, CDFW 2009). According to Dryfoos (1965), the San Francisco Estuary (San Francisco Bay and Sacramento-San Joaquin River Delta) population has been considered the largest and southernmost self-sustaining population along the U.S. Pacific Coast, and has been considered to be genetically isolated from other populations (McAllister 1963, Moyle 2002). Once one of the most abundant species observed in Estuary surveys (Moyle et al. 2011), the Estuary longfin smelt (LFS) population has experienced dramatic declines over several decades (Rosenfield and Baxter 2007, Sommer et al. 2007, Baxter et al. 2008, Thomson et al. 2010), resulting in its March 2009 inclusion in the list of threatened pelagic fish species under the California Endangered Species Act (CDFW 2009).

A number of studies have investigated LFS distribution, habitat, and life history characteristics within the Estuary (Baxter 1999, Dege and Brown 2004, Hobbs et al. 2006, CDFW 2009, Moyle 2002, Matern et al. 2002, Rosenfield and Baxter 2007, Kimmerer et al. 2009, MacNally et al. 2010, Thomson et al. 2010). However, most of what has been learned about LFS (e.g., growth and in-river residence times) comes from other locations across its range, most often from Lake Washington (Dryfoos 1965, Eggers et al. 1978, Moulton 1979, Chigbu 1993, Chigbu and Sibley 1994a, 1994b, Chigbu and Sibley 1998, Chigbu et al. 1998, Chigbu 2000, Chigbu and Sibley 2002). Potential factors associated with abundance changes in Estuary fish species include stock-recruitment effects, increased mortality rates, reduced prey availability, overall shifts in fish assemblage composition (Feyrer et al. 2003, Sommer et al. 2007), and altered location of the 2 ppt isohaline in spring (known as "X2"; Thomson et al. 2010). Furthermore, the cascading impacts of aquatic species invasions can change food webs and make management actions for native fish more difficult (Feyrer et al. 2003).

Rosenfield and Baxter (2007) assessed the Estuary LFS population and addressed questions about distribution patterns and population dynamics. They used data from three long-term aquatic sampling programs of the California Department of Fish and Wildlife (CDFW; formerly California Department of Fish and Game) (i.e., Fall Midwater Trawl [FMWT], Bay Study Midwater Trawl [BMWT] and Otter Trawl [BOT]) and the University of California, Davis's Suisun Marsh survey that captured LFS from upstream of the Sacramento and San Joaquin River confluence to San Francisco Bay, to assess distribution and abundance, and tested for differences in abundance during pre-drought (1975–1986), drought (1987–1994) and post-drought (1995–2007) periods. Rosenfield and Baxter (2007) indicated significant declines in LFS abundance among these time periods, supporting their hypothesis that the Estuary's capacity to maintain pelagic fish species has been reduced over the past three decades. These results provide critically important information on distribution and abundance dynamics for LFS within the Estuary. However, questions remain about the full geographical extent and frequency of occurrence within the Estuary of each LFS life stage.

A full spatial depiction of where and when LFS are observed is vital to our understanding of critical management issues, including identifying important regions for each life stage, and potential opportunities for population conservation. In addition, when planning a conservation strategy for species protection and restoration, the spatial distribution of each population is required under federal and state statutes (Tracy et al. 2004, Carroll et al. 2006, Merz et al. 2011). Finally, considering data in a life stage-specific context provides for future assessment of stage-specific effects, supporting more practical and informative evaluations of specific cause–effect relationships, and will permit quantifying relationships between specific life stage transitions and environmental parameters (Merz et al. 2013). Interactive maps of some monitoring programs from CDFW have been publicly available for individually captured and monitored fish species, including LFS distribution within the Estuary (see http://www.dfg.ca.gov/delta). However, to our knowledge, no effort has been made to map LFS spatial range and distribution by life stages using available Estuary sampling data. The goal of this paper is to provide a comprehensive description of the range and temporal and geographic distribution of LFS by life stage within the Estuary.

Methods

Study area.—The San Francisco Estuary is the largest urbanized estuary (approximately 1,235 km^2) on the west coast of the United States (Lehman 2004, Oros and Ross 2005) (Figure 1). It consists of a series of basins with three distinct segments that drain an area of approximately 163,000 km^2 (40% of California's surface area): the Delta, Suisun Bay, and San Francisco Bay (van Geen and Luoma 1999, Sommer et al. 2007). The uppermost region of the Estuary is the delta of the Sacramento and San Joaquin rivers (Delta), a complex and meandering network of tidal channels around leveed islands (Moyle 2002, Kimmerer 2004). These two rivers narrow and converge before connecting with Suisun Bay, a large, shallow and highly productive expanse of brackish water that is strongly influenced by ebb and flood tides. Adjacent to Suisun Bay, Suisun Marsh, the largest contiguous brackish water wetland in the Estuary, provides a fish nursery area and habitat for migratory birds (Moyle 2002, Sommer et al. 2007). Suisun Bay is connected to San Pablo Bay — a northern extension of San Francisco Bay — through a long narrow channel called the Carquinez Strait. During high outflow years, the San Francisco Bay's salinity levels can be somewhat diluted by freshwater allowing freshwater fishes to move into tributary streams (Moyle 2002).

To qualitatively describe the spatial distribution of LFS, we delineated the Estuary into 22 regions (Figure 1, Table 1). These regions were South San Francisco Bay (1); Central San Francisco Bay (2); West San Pablo Bay (3); East San Pablo Bay (4); Lower Napa River (5); Upper Napa River (6); Carquinez Strait (7); Suisun Bay Southwest (8); Suisun Bay Northwest (9); Suisun Bay Southeast (10); Suisun Bay Northeast (11); Grizzly Bay (12); Suisun Marsh (13); Confluence (14); Lower Sacramento River (15); Upper Sacramento River (16); Cache Slough and Ship Channel (17); Lower San Joaquin River (18); East Delta (19);

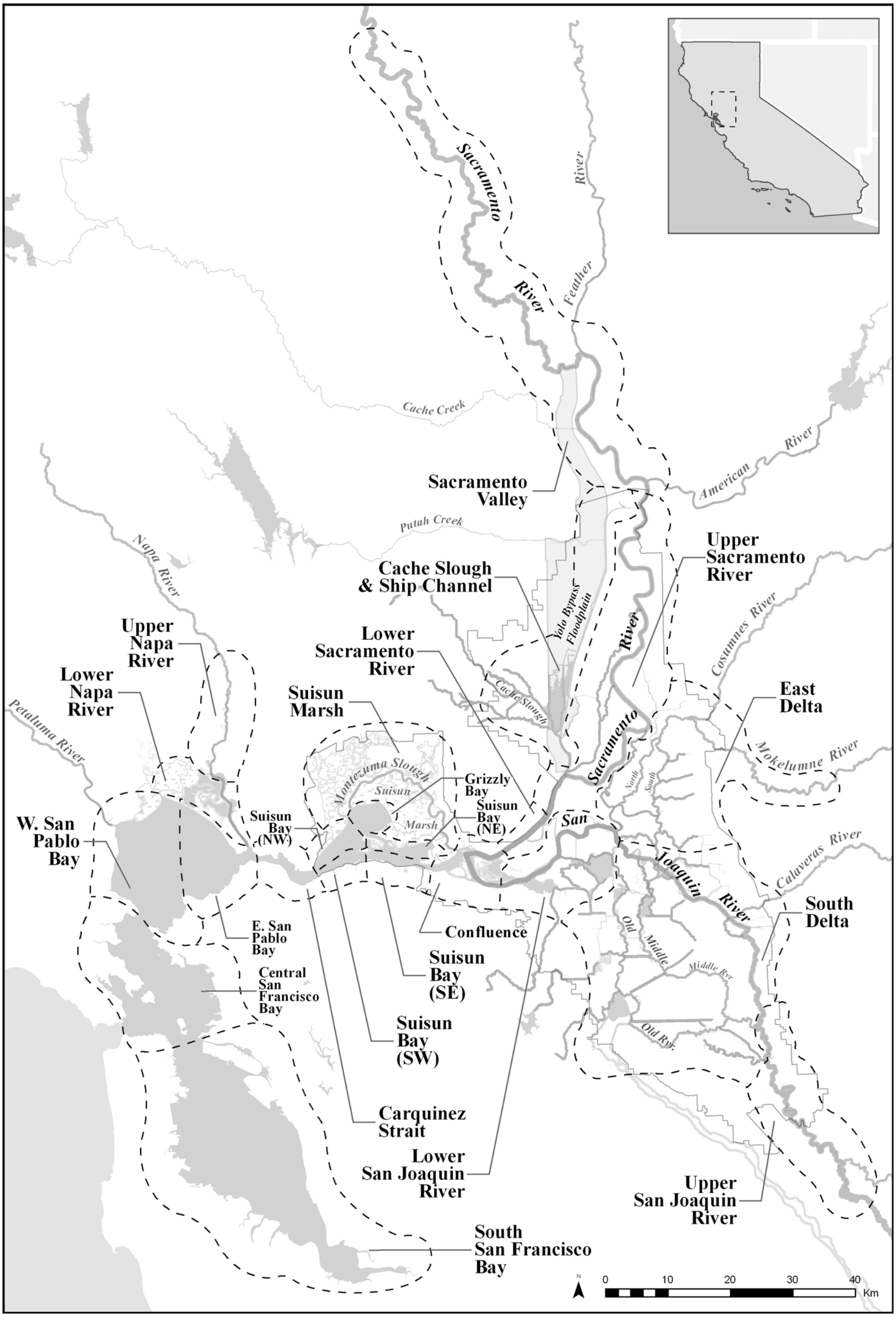

Figure 1.—A map of the San Francisco Estuary, California, and the 22 regions identified in this paper. Dashed lines indicate the estuary's regional delineations, which was based on the physical habitat and flow characteristics as well as physical landmarks (Kimmerer 2009, Merz et al. 2011).

Table 1.—Interagency Ecological Program (IEP) and Regional Monitoring Program (RMP) data that are publicly available, and were used to establish longfin smelt geographical extent range in the San Francisco Estuary, California.

Location	Survey Name	Gear Used	Study Period	Agency/ Sources	Program
Sacramento-San Joaquin Delta, Sacramento River, Chipps Island, San Francisco Estuary, Mossdale Crossing	Chinook and POD[a] Species	Beach Seine, Midwater Trawl, Kodiak Trawl	1976 - present	USFWS[b]	IEP
San Pablo Bay, Suisun Bay, Sacramento-San Joaquin Delta	20mm Survey	20-mm Plankton Net	1995 - present	CDFG[c]	IEP
Delta, Suisun Bay and Suisun Marsh	Smelt Larval Survey	Egg and Larval Net	2009 - present	CDFG[c]	IEP
San Pablo Bay, Suisun Bay, Sacramento-San Joaquin Delta, Sacramento Deep Water Ship Channel	Spring Kodiak Trawl	Kodiak Trawl	2002 - present	CDFG[c]	IEP
San Pablo Bay, Suisun Bay, Sacramento-San Joaquin Delta, Sacramento Deep Water Ship Channel	Fall Midwater Trawl	Midwater Trawl	1967 - present	CDFG[c]	IEP
San Pablo Bay, Suisun Bay, Sacramento-San Joaquin Delta, Sacramento Deep Water Ship Channel	Summer Tow Net Survey	Tow Net	1959 - present	CDFG[c]	IEP
San Francisco Bay, San Pablo Bay, Suisun Bay and downstream of Sacramento-San Joaquin Delta	San Francisco Bay Study	Midwater Trawl, Otter Trawl	1980 - present	CDFG[c]	IEP

TABLE 1 (continued).

Location	Survey Name	Gear Used	Study Period	Agency/ Sources	Program
San Francisco Bay, San Pablo Bay, Suisun Bay and downstream of Sacramento-San Joaquin Delta	San Francisco Plankton Net	Larval/Plankton Net	1980 - 1989	CDFG[c]	IEP
State Water Project and Central Valley Water Project	Fish Salvage Monitoring	Sieve Net	1993-present	CDFG[c]	IEP
Northern Sacramento-San Joaquin Delta	North Bay Aqueduct Survey	Larval Net	1995-2004	CDFG[c]	IEP
Suisun Marsh	Suisun Marsh Monitoring	Beach Seine, Larval Sled, Midwater Trawl, Otter Trawl	1980 - present	DWR[d] - UC Davis	IEP
Yolo Bypass	Yolo Bypass Study	Beach Seine	1998-2005	DWR[d]	RMP
Yolo Bypass	Yolo Bypass Study	Fyke Net	1998	DWR[d]	RMP
Yolo Bypass	Yolo Bypass Study	Fyke Trap	1999-2005	DWR[d]	RMP
Yolo Bypass	Yolo Bypass Study	Purse Seine	1998	DWR[d]	RMP
Yolo Bypass	Yolo Bypass Study	Rotary Screw Trap	1998-2005	DWR[d]	RMP
Yolo Bypass	Yolo Bypass Floodplain Study	Rotary Screw Trap	1999-2002	Sommer et al. 2004	RMP

TABLE 1 (continued).

Location	Survey Name	Gear Used	Study Period	Agency/ Sources	Program
Sacramento-San Joaquin Delta	Littoral Fish Assemblages	Electrofishing	1980-2000	Brown & Michniuk 2007	RMP
Mokelumne River	Salmon and Steelhead Monitoring	Rotary screw trap	1993-2004	EBMUD[e]	RMP
Central Delta	Distribution of native and alien ichthyoplankton	Ichthyoplankton net	1990-2000	Grimaldo et al. 2004	RMP
Suisun Marsh	Native Alien Fishes	Beach Seine, Otter Trawl	1979-1999	Matern et al. 2002	RMP
Cosumnes River	Floodplain monitoring: Native and Alien Fish	Seine, Electrofishing	1998-2005	Moyle et al. 2007	RMP
Cosumnes River	Stream Evaluation	Seining, Rotary Screw Trap	1990-2000	Snider & Titus 2000	RMP
Cosumnes River	Larval Fishes on a restored Floodplain	Light traps, Dip nets	1999 - 2001	Crain et al. 2004	RMP
Lower Mokelumne River	Fish Community Survey	Seining, Backpack and Boat Electrofishing	1997-2004	Merz & Saldate 2000, 2005	RMP
Sacramento-San Joaquin Delta	Fishes of the Delta	Otter Trawl	1963-1964	Radtke 1966	RMP

Table 1 (continued).

Location	Survey Name	Gear Used	Study Period	Agency/ Sources	Program
Liberty Island	Spatial and temporal patterns by native and non-native fish larvae of a recently flooded island	Light traps, larval trawls	2003-2005	Marshall et al. 2006	RMP
South-east Suisun Bay, Confluence Sacramento and San Joaquin Rivers	Delta Mirant Power Plants	Sieve Net	2006 - 2008	Pittsburg and Contra Costa Power Plants	RMP
Lower Calaveras River	Calaveras River Barrier Removal	Beach Seine	2010	T.Kennedy[f]	RMP
West Delta	West Delta Survey	Beach Seine	2005-2006	T.Kennedy[f]	RMP

[a]POD: Pelagic Organism Decline
[b]USFWS: United States Fish and Wildlife
[c]CDFG: California Department of Fish and Game
[d]DWR: Department of Water Resources
[e]EBMUD: East Bay Municipal Utility District
[f]Fishery Foundation of California, personal communication

South Delta (20); Upper San Joaquin River (21); and Sacramento Valley (22). Delineation of Estuary regions was based on physical habitat, flow characteristics, and physical landmarks described in Kimmerer (2009) and Merz et al. (2011).

Monitoring data.—We synthesized all available information on Estuary fish monitoring surveys from the 1960s through 2012. These data were obtained directly from governmental and non-governmental entities, published and unpublished papers or reports, and through publicly available online databases of different surveys (i.e., http://www.water.ca.gov/iep/products/data.cfm). All data were reviewed and classified into either the Interagency Ecological Program (IEP) or the Regional Monitoring Program (RMP).

Interagency Ecological Program (IEP).—The Interagency Ecological Program (IEP) is a consortium of federal and state agencies that conducts long-term biological and ecological monitoring for use in Estuary management (Table 1). These monitoring surveys were from the United States Fish and Wildlife Service (USFWS) for Chinook salmon and pelagic organism decline (POD) species; CDFW for 20-mm plankton-net (20mm), Smelt Larval Survey (SLS), Spring Kodiak trawl (Kodiak), Fall midwater trawl (FMWT), Summer tow net, North Bay Aqueduct, Fish Salvage, San Francisco Bay Study's midwater trawl and Bay otter trawl (BOT), and San Francisco plankton net (Bay Plankton); and,California Department of Water Resources (CDWR) and the University of California Davis (UCD) for the Suisun Marsh monitoring. The IEP monitoring program is conducted using different sampling periods (e.g., biweekly, monthly), during different seasons and sampling frequency (e.g., Fall midwater trawl, Spring Kodiak trawl, Summer Tow Net), and on some occasions at a varying number of stations (i.e., supplemental stations are sometimes added for special study, or changes occurred depending on funding). Explicit, detailed descriptions for each IEP monitoring survey are available at the IEP website (http://www.water.ca.gov/iep/products/data.cfm).

Regional Monitoring Program (RMP).—Surveys conducted on a smaller geographic scale of the Estuary, and oftentimes in a shorter time period compared to the IEP surveys were classified in this study as RMP surveys (Table 1). The RMP surveys were carried out by various research institutions and governmental entities, and for a variety of project purposes (e.g. fish community survey, distribution and abundance, fish monitoring, floodplain monitoring). We summarized the number of sampling stations within each of the 22 identified regions, and identified the percentage of regions sampled by each survey (Table 2).

Observed geographic extent.—We utilized IEP and RMP survey records to identify the geographical extent of LFS within the Estuary. Following the approach of Merz et al. (2011) in developing the extent range of delta smelt (*Hypomesus transpacificus*) we used ArcGIS version 10 (ESRI, Redlands, CA) to plot all surveyed stations from the different monitoring programs from the 1960s through 2012 (Figure 2). If LFS were detected at least once at any given monitoring station, the species was designated as present at that site; otherwise the site was designated as "not observed" (Figure 2). We then developed a boundary around the stations where LFS were detected using a 1-km buffer (Merz et al. 2011, Graham and Hijmans 2006). We also calculated the total surface area of all waters within the range where LFS were observed using the ArcGIS 10 geoprocessing calculation tool (http://www.esri.com/software/arcgis/arcgis10). Note that the LFS geographical extent developed in this study did not consider the species to be absent if LFS were not observed, because of the lack of information on detection probability and different sampling frequencies for each survey gear type (Merz et al. 2011, Pearce and Boyce 2006).

Table 2.—The San Francisco Estuary regions and associated number of monitoring stations by sampling gears and monitoring surveys. "NS" = not sampled and "NI" = no regional sampling identified. San Francisco Estuary, California.

	Interagency Ecological Program Surveys										
	CDFG Monitoring Surveys								USFWS	DWR-UC Davis	Regional Surveys
Region	Spring Kodiak Trawl	20mm Survey	Summer Tow Net Survey	Delta Fall Midwater Trawl	Smelt Larva Survey	Smelt Larval Survey	SF Bay Study	Fish Salvage	Chinook and POD Surveys	Suisun Marsh Surveys	
South San Francisco Bay	NS	NS	NS	1	NS	NS	48	NS	NS	NS	NI
Central San Francisco Bay	NS	NS	NS	2	NS	NS	32	NS	10	NS	NI
West San Pablo Bay	NS	NS	3	22	NS	NS	20	NS	4	NS	NI
East San Pablo Bay	NS	7	8	17	NS	7	20	NS	4	NS	NI
Lower Napa River	2	3	4	2	NS	3	NS	NS	0	NS	NI
Upper Napa River	4	7	1	NS	NS	7	NS	NS	0	NS	NI
Carquinez Strait	1	1	3	8	1	1	8	NS	6	NS	NI
Suisun Bay (SW)	1	1	1	5	1	1	4	NS	1	NS	NI
Suisun Bay (NW)	1	1	1	6	1	1	12	NS	0	NS	NI
Suisun Bay (SE)	2	2	2	8	2	2	4	NS	2	NS	1
Suisun Bay (NE)	2	2	2	5	2	2	4	NS	0	NS	NI
Grizzly Bay	1	1	1	4	1	1	4	NS	0	NS	NI
Suisun Marsh	5	3	3	5	3	3	NS	NS	9	93	10
Confluence	4	5	4	13	5	5	8	NS	11	NS	41
Lower Sacramento	4	4	3	4	4	4	6	NS	0	NS	36
Upper Sacramento	4	3	2	13	1	1	6	NS	51	NS	10
Cache Slough/Ship Channel	5	11	1	10	2	1	0	NS	11	NS	17
Lower San Joaquin River	6	6	4	13	5	6	12	NS	15	NS	34
East Delta (Mokelumne)	5	1	2	8	1	1	0	NS	26	NS	51
South Delta	6	9	7	15	6	6	0	3	50	NS	15
Upper San Joaquin River	NS	NS	NS	NS	NS	NS	0	NS	23	NS	2
Sacramento Valley	NS	NS	NS	NS	NS	NS	0	NS	53	NS	6
Total number of stations surveyed	53	67	52	161	35	52	188	3	276	93	223
Percent of regions represented	73	77	82	86	64	77	86	5	95	5	50

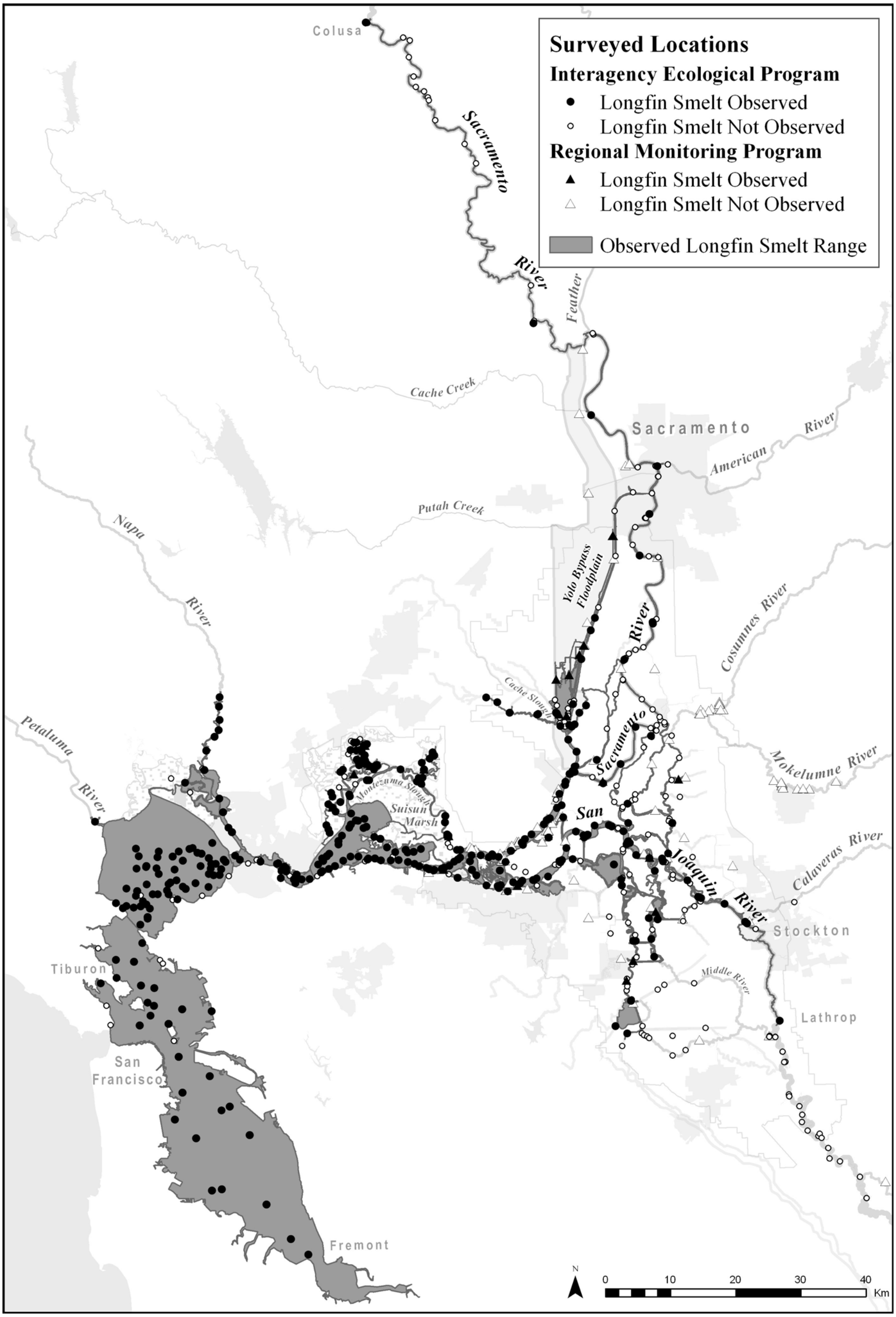

Figure 2.—The geographical extent range and observations of longfin smelt at monitoring stations of Interagency Ecological Program (IEP) survey and Regional Monitoring Program (RMP) surveys. Circles indicate IEP stations where longfin smelt were observed (closed) or not observed (open). Triangles indicate RMP stations where longfin smelt where observed (closed) or not observed (open). The dark gray represents the observed longfin smelt range in the San Francisco Estuary, California.

Table 3.—Delineations of longfin smelt lifestages by time-period, sizes, IEP sampling gears and sampling periods, and descriptions used for frequency of detection analysis in the San Francisco Estuary, California.

Life Stage	Time Period	Sizes	Sampling Study[1]	Sampling Years	Sampling Months	Description
Larva	Jan -June	<16 mm	Bay Plankton 20mm SLS	1980-1989 1995-2011 2009-2011	Jan-June Mar-May Jan-Mar	The larval phase begins after hatching and ends when resorption of the yolk-sac and fin formation are nearly complete (< 16mm; Wang 1991).
Juvenile	Apr-Oct	Baxter (2009) monthly cutoffs	BOT 20mm FMWT	1980-2011 1995-2011 1980-2011	Apr-Oct Apr-Jul Sep-Oct	This phase begins when fin formation is nearly complete (16mm; Wang 1991), and encompasses the first major growth period of longfin smelt (Moyle 2002).
Sub-adult	Nov-Apr	Baxter (2009) monthly cutoffs	BOT FMWT Kodiak	1980-2011 1980-2011 2002-2011	Nov-Apr Nov-Dec Jan-Apr	Period of slow-growth during winter months (Moyle 2002) prior to anadromous migration.
Anadromous	Mar-Jan	Baxter (2009) monthly cutoffs	BOT	1980-2011	Mar-Jan	Encompasses second major growth period (Moyle 2002) and period of anadromous outmigration for a portion of the population towards the ocean from March through August and immigration upstream from September through January (Rosenfield and Baxter 2007).
Adult	Dec-May	Baxter (2009) monthly cutoffs	BOT Kodiak	1980-2011 2002-2011	Dec-May Jan-May	Encompasses spawning period of adult longfin smelt (Moyle 2002). Gravid females are detected between late-fall and winter (Rosenfield 2010; Moyle 2002)

[1]Bay Plankton = San Francisco Plankton Net Survey, 20mm = 20mm survey, SLS = Smelt Larval Survey, BOT = San Francisco Bay Study Otter Trawl, FMWT = Fall Midwater Trawl, and Kodiak Trawl = Spring Kodiak Trawl.

Life stage determinations.—We delineated life stages based on month and fish-size (Table 3, Figure 3). We adapted LFS life-stage definitions and monthly cut-offs established by DRERIP (Delta Regional Ecosystem Restoration Implementation Plan; Rosenfeld 2010). LFS life stages used in this study are *larva, juvenile, sub-adult, anadromous,* and *adult* (Table 3, Figure 3). Unlike DRERIP (Rosenfield 2010), we defined an anadromous stage to highlight the LFS migratory period (Rosenfield and Baxter 2007), and defined an adult life stage instead of "sexually mature adult" due to unavailability of sexual maturation data to differentiate premature versus mature LFS. We also did not evaluate the egg life stage as there are no Bay-Delta surveys (e.g., plankton net) that monitor LFS eggs. Because the

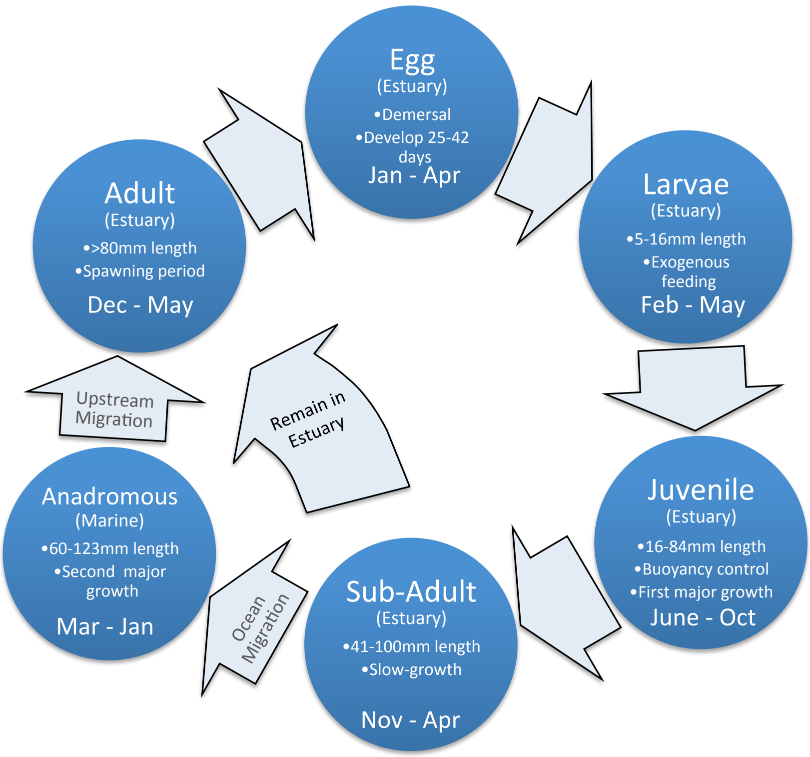

Figure 3.—Life cycle of longfin smelt, adapted from the Delta Regional Ecosystem Restoration Implementation Plan (DRERIP) Conceptual Models. Available at: http://www.dfg.ca.gov/erp/cm_list.asp

LFS life cycle spans 3 calendar years, we used the monthly fork length criteria defined by Baxter (1999) to separate LFS of each age (years 1, 2, or 3; Table 4). The only modification of Baxter's (1999) criteria is the addition of a maximum length cutoff of 15 mm for larva, which is the length at which yolk-sac resorption and fin formation are nearly complete (Wang 1991; Table 4).

Table 4.—Length (mm) delineations of longfin smelt by year, life stage, and month used in frequency of detection analyses. Monthly length cut-offs from Baxter (1999), except for 16-mm cutoff for larva used to separate larvae and juveniles. San Francisco Estuary, California.

Year 1			Year 2			Year 3		
Life Stage (s)	Month	FL (mm)[1]	Life Stage (s)	Month	FL (mm)	Life Stage (s)	Month	FL (mm)
Larva	Jan	<16	Sub-adult	Jan	40-89	Anadromous, Adult	Jan	>89a
Larva	Feb	<16	Sub-adult	Feb	42-92	Adult	Feb	>92
Larva	Mar	<16	Sub-adult, Anadromous	Mar	46-95[2]	Adult	Mar	>95
Larva, Juvenile	Apr	<16, 16-51	Sub-adult, Anadromous	Apr	52-99[2]	Adult	Apr	>99
Larva, Juvenile	May	<16, 16-58	Anadromous	May	59-104	Adult	May	>104
Larva, Juvenile	Jun	<16, 16-66	Anadromous	Jun	67-107			
Juvenile	Jul	<71	Anadromous	Jul	71-110			
Juvenile	Aug	<75	Anadromous	Aug	75-113			
Juvenile	Sep	<80	Anadromous	Sep	80-116			
Juvenile	Oct	<83	Anadromous	Oct	83-119			
Sub-adult	Nov	<85	Anadromous	Nov	85-122			
Sub-adult	Dec	<87	Anadromous, Adult	Dec	87-124[2]			

[1] FL = Fork length
[2] Length range applied to both life stages

During the first year of life, LFS transition from egg (December–April; Rosenfield 2010) to free-floating, endogenously nourished larva (January–June; Rosenfield 2010), to juvenile when the first major growth period occurs (April–October; Moyle 2002), and to sub-adult when growth slows during winter months prior to anadromous migration (November–December; Moyle 2002). Unlike DRERIP (Rosenfield 2010), which describes the juvenile stage as extending until the end of the first year of life, we cut off the life stage in October, at the end of the first major growth period as described by Moyle (2002). Additionally, instead of the sub-adult stage extending from the beginning of the second year of life to maturation (Rosenfield 2010), we defined the sub-adult period as the winter, slow-growth period between the juvenile and anadromous life stages.

The second and third years of life begin with the slow-growth period of sub-adults continuing into spring (January–April; Moyle 2002). Next, a portion of the LFS population undertakes an anadromous migration (emigration) towards the ocean, followed by return upstream migration (immigration) during March–January (Rosenfield and Baxter 2007), while remaining LFS continue to rear in the Estuary. This summer and fall period encompasses the second major LFS growth period (Moyle 2002). Finally, the LFS adult life stage encompasses the spawning period during December–May (Rosenfield 2010; Moyle 2002).

Frequency of detection. —Because each type of gear selectively captures different LFS life stages and is deployed in different seasons, we used data from six IEP monitoring surveys (Bay Plankton, 20mm, SLS, BOT, Kodiak trawl, and FMWT) to examine LFS spatial distribution across life stages within the Estuary (Table 3). For each life stage, only data from each gear type that fell within delineated months for that life stage were used (Table 3). We used LFS catch data for years 1980 to 2011 for all surveys except for 20mm, SLS and Kodiak, where sampling started in 1995, 2009 and 2002 respectively (Table 3). We included only sampling stations that were consistently surveyed, as determined by identifying stations that were sampled ≥90% of the time across all years (Merz et al. 2011).

The average annual LFS detection frequency at consistently surveyed stations for each life stage (except anadromous stage) in each region was calculated as

$$P_{lrpy} = (S_{lrpy} / N_{rpy}) * 100$$

where P_{lrpy} represents the percent of unique numbers of sampling events in which the life stage *l* LFS were captured in each region *r* during time period *p* and year *y*; S_{lrpy} represents the number of sampling events in a region *r* when the life stage *l* LFS were captured during time period *p* and year *y*; and, N_{rpy} represents the total number of sampling events from region *r* during time period *p* and year *y*. Next, the average annual frequency of observation for LFS by life stage and region was calculated as a simple average over all years. Results from LFS detection frequencies by life stage (except anadromous stage) and region were mapped using ArcGIS 10.

Because a portion of the Estuary LFS population migrates during the anadromous life stage, detection frequency was calculated monthly within regions to better depict LFS migratory movements. Similar methods employed for the other life stages were used to calculate detection frequency for the anadromous life stage, except time period *p* was monthly, and regions *r* were grouped into four areas (Lower Rivers, Suisun, East Bay, and West Bay) to better visualize anadromous behavior. Lower Rivers covers all regions from Sacramento Valley downstream to the Lower Sacramento River and San Joaquin River regions, Suisun covers the Confluence and all Suisun Bay regions, East Bay covers Carquinez Straight downstream to East San Pablo Bay, and West Bay covers the West San Pablo Bay and San Francisco Bay regions.

Results

Within the 22 Estuary regions, we identified 357,538 survey events (a sampling event at a given location and time) at 1,203 monitoring stations. Of these, 343,482 (96%) were from IEP and 14,056 (4%) were from regional monitoring programs (Table 1). The program or survey with the single greatest number of monitoring stations was the Chinook and POD (276), followed by the SF Bay Study (188), FMWT (161), Suisun Marsh surveys (93), 20mm Survey (67), and Spring Kodiak Trawl (53) (Table 2). A total of 1,035,183 LFS were observed at 620 of the 980 (63%) IEP monitoring stations and at 23 of the 223 (10%) regional monitoring stations identified in this study.

Observed geographic extent.—LFS were observed in all 22 regions covering an area of about 137,500 ha (Figure 2). Observations occurred as far west as Tiburon in Central San Francisco Bay, north as far as the town of Colusa on the Sacramento River (Sacramento Valley region), east as far as Lathrop on the San Joaquin River (border of South Delta and San Joaquin River regions), and south as far as the Dumbarton Bridge in South San Francisco Bay. Tributary observations included the Napa and Petaluma rivers, Cache Slough, and the Mokelumne River to the east. LFS were also observed in seasonally-inundated habitat of the Yolo Bypass.

No single IEP monitoring program sampled all 22 regions (Table 2) that make up the observed extent of LFS range, and three regions had no IEP sampling. The Chinook and POD surveys had the highest coverage (95% of regions each). The FMWT and SF Bay surveys covered 86% of the regions each, while coverage among the other IEP surveys ranged from 5 to 82%. Each RMP survey typically covered less than 4% of the observed extended range.

Distribution by life stage.— For all life stages, LFS were observed most frequently throughout a relatively large portion of their range – from East San Pablo Bay north into Suisun Marsh down through Grizzly Bay, and all four regions of Suisun Bay through the Confluence (Figure 4, Figure 5). In addition to being frequently detected in the central

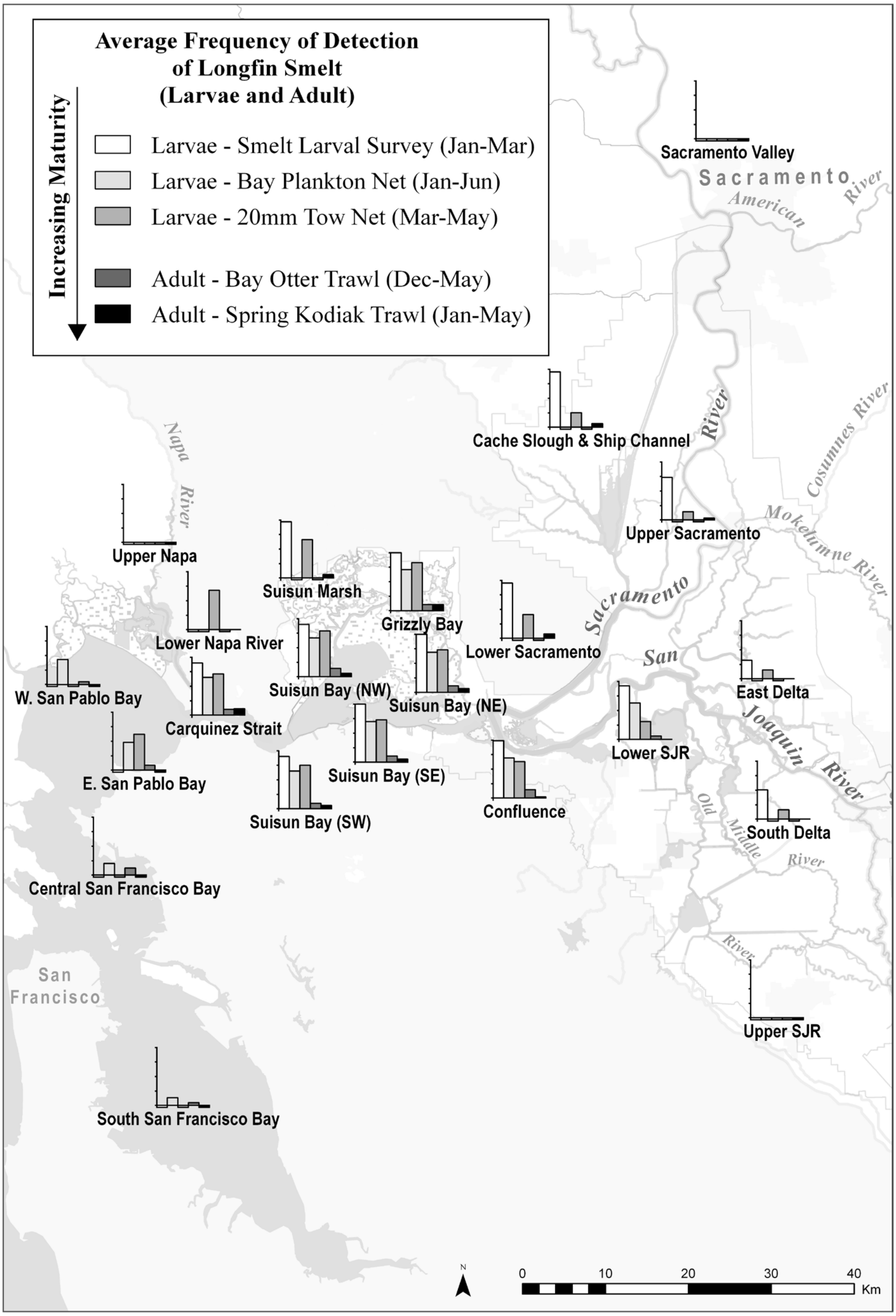

FIGURE 4.—Average annual frequency of longfin smelt detection (%) for larvae and adult lifestages by region and Interagency Ecological Program survey type. The percent of sampling events where longfin smelt was observed over the total number of sampling events within a region. Regions where the percent frequency of detection for a given life stage was zero is indicated by no data column/bar being present in the bar graph. Regions that were not sampled for a given life stage are indicated by a data column/bar suspended slightly below the x-axis. Y-axis ticks indicate percent frequencies of 0, 25, 50, 75 and 100 percent.

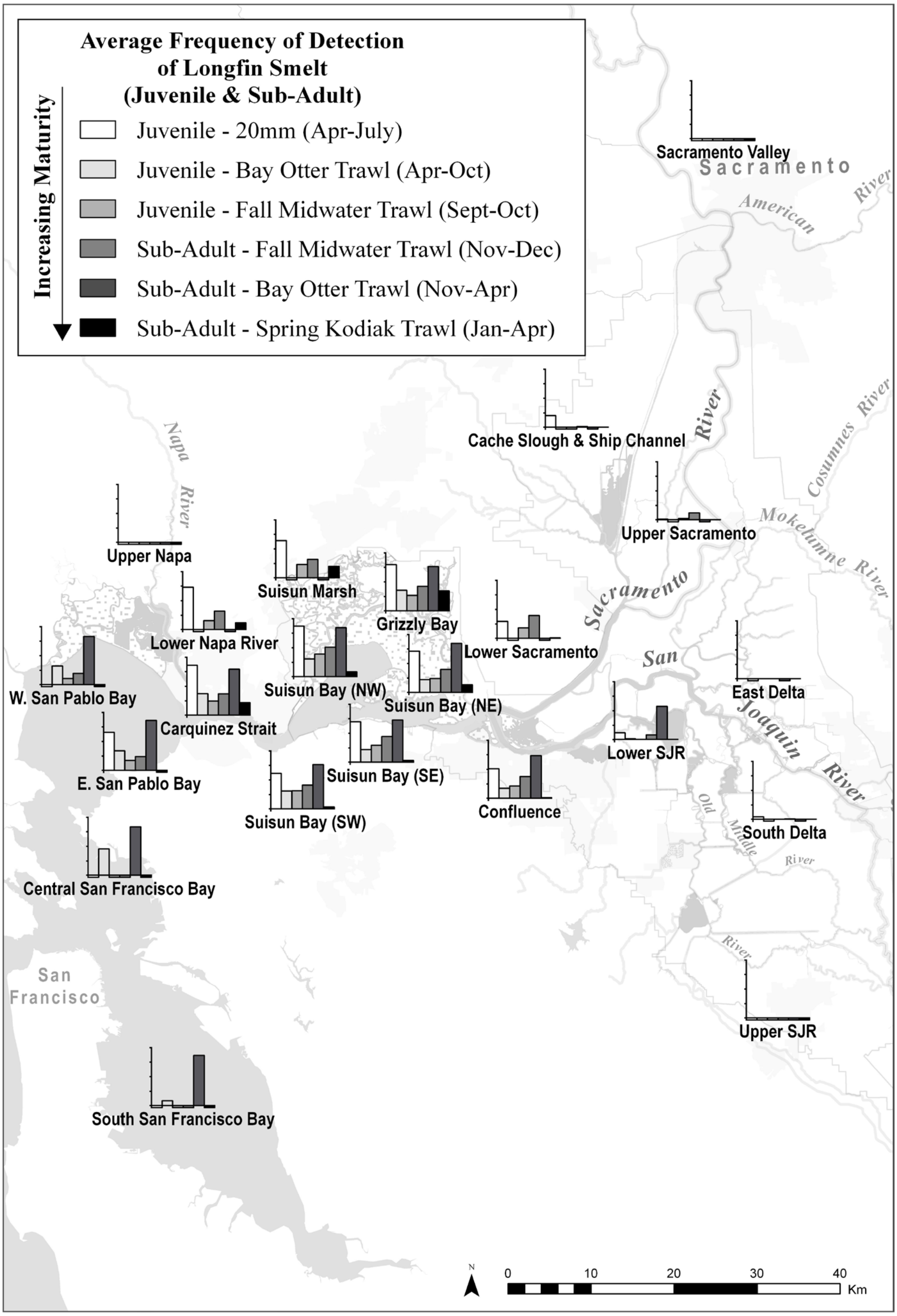

Figure 5.—Average annual frequency of longfin smelt detection (%) for juvenile and sub-adult life stages by region and Interagency Ecological Program survey type. The percent of sampling events where longfin smelt was observed over the total number of sampling events within a region. Regions where the percent frequency of detection for a given life stage was zero is indicated by no data column/bar being present in the bar graph. Regions that were not sampled for a given life stage are indicated by a data column/bar suspended slightly below the x-axis. Y-axis ticks indicate percent frequencies of 0, 25, 50, 75 and 100 percent.

regions (from Carquinez Straight upstream to the Confluence), adult and larvae were both detected relatively frequently upstream of the Confluence (Figure 4, Table 5). Larvae were detected greater than 73% of the time in the Lower Sacramento, Upper Sacramento, Cache Slough and Ship Channel, and Lower San Joaquin regions, and greater than 31% of the time in the East Delta and South Delta regions during the SLS (Figure 4, Table 5). Although detected at a much lower frequency across all regions than larvae, adults were also detected in South San Francisco Bay, upstream in Cache Slough and Ship Channel, and Upper Sacramento regions.

Unlike adult and larval life stages, juvenile and sub-adult life stages were not frequently detected upstream of the Confluence, and instead were more frequently detected in the most downstream Bay regions (Figure 5, Table 5). During BOT sampling, juveniles and sub-adults were detected in greater than 32% of sampling events in both San Pablo Bay regions and Central San Francisco Bay. Sub-adults were also detected at a relatively high frequency (86.6%) in the South San Francisco Bay during BOT sampling (Figure 5, Table 5).

During the anadromous life stage, LFS exhibited declining average frequency of detection during the spring months and into mid-summer, followed by increasing average detection frequency throughout the fall months across all Estuary areas during BOT sampling (Figure 6). The lowest average detection frequencies for each area occurred at successively

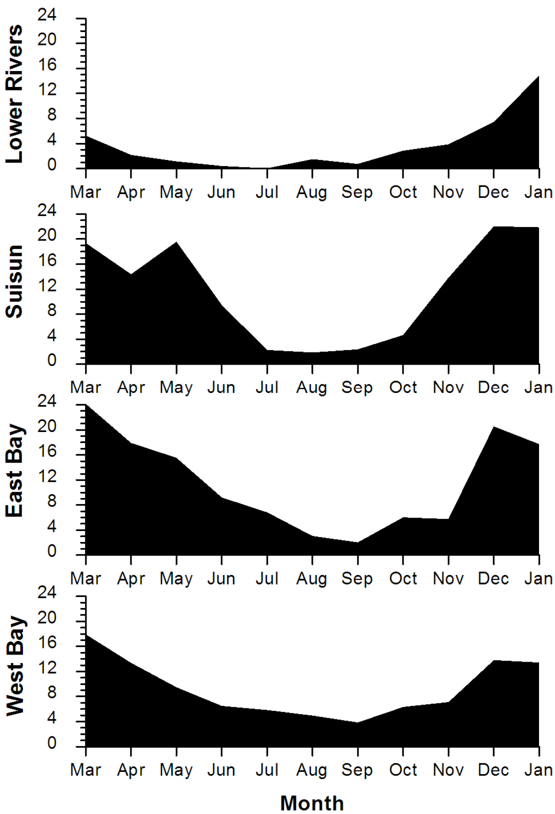

FIGURE 6.—Average annual frequency of longfin smelt detection (%) for the anadromous life stage by month and area for the years 1980–2011. Frequency of detection was calculated as the percent of sampling events where longfin smelt were observed over the total number of sampling events within an area. Lower Rivers covers all regions from Sacramento Valley downstream to the Lower Sacramento and San Joaquin River regions, Suisun covers the Confluence and all Suisun Bay regions, East Bay covers Carquinez Straight downstream to East San Pablo Bay, and West Bay covers West San Pablo Bay and San Francisco Bay regions.

Table 5.—Average frequency (%) of longfin smelt detection by life-stage across all years, Interagency Ecological Program monitoring program, and region in the San Francisco Estuary, California.

	Life-Stage										
	Larvae			Juvenile			Sub-Adult			Adult	
Monitoring Program[1]	BP	20mm	SLS	BOT	20mm	FMWT	BOT	FMWT	Kodiak	BOT	Kodiak
Years of data used	80-89	95-11	09-11	80-11	95-11	80-11	80-11	80-11	02-11	80-11	02-11
Time Period	Jan-Jun	Mar-Jun	Jan-Mar	Apr-Oct	Apr-Jul	Sep-Oct	Nov-Apr	Nov-Dec	Jan-Apr	Dec-May	Jan-May
Region											
South San Francisco Bay	13.0	ns[2]	ns	8.2	ns	ns	86.6	ns	ns	4.7	ns
Central San Francisco Bay	20.0	ns	ns	45.6	ns	ns	83.6	ns	ns	12.1	ns
West San Pablo Bay	43.0	ns	ns	32.1	ns	10.4	82.6	19.1	ns	4.7	ns
East San Pablo Bay	48.0	62.0	ns	33.5	65.4	17.0	85.9	23.4	ns	8.7	ns
Lower Napa River	ns	68.0	ns	ns	73.0	15.6	ns	31.8	11.7	ns	0.0
Upper Napa River	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Carquinez Strait	65.0	71.0	90.0	37.0	86.1	24.2	79.2	36.6	21.7	9.7	11.0
Suisun Bay (SW)	65.0	75.0	90.0	30.7	61.0	31.1	76.0	40.9	3.3	9.4	5.8
Suisun Bay (NW)	67.0	79.0	90.0	30.7	87.1	39.1	84.6	50.9	8.3	14.1	5.8
Suisun Bay (SE)	70.0	73.0	100.0	21.8	69.9	29.3	72.6	44.2	2.9	10.3	5.3
Suisun Bay (NE)	69.0	73.0	100.0	21.8	70.9	23.8	84.4	39.5	12.9	11.1	6.3
Grizzly Bay	71.0	83.0	100.0	35.1	79.3	26.3	76.2	42.1	34.2	10.7	10.7
Suisun Marsh	ns	66.0	96.7	ns	64.4	22.9	ns	31.8	19.7	ns	5.8
Confluence	69.0	63.0	99.0	16.8	50.7	21.0	73.3	37.3	0.8	14.4	2.2
Lower Sacramento	ns	41.0	95.4	ns	29.2	18.0	ns	39.5	0.8	ns	7.7
Upper Sacramento	ns	14.0	73.3	ns	0.9	2.0	ns	11.9	0.0	ns	3.3
Cache Slough & Ship Channel	ns	25.0	95.4	ns	19.8	ns	ns	0.8	0.0	ns	6.4
Lower San Joaquin River	63.0	31.0	92.3	1.0	11.5	0.2	57.1	8.0	0.0	5.9	0.0
East Delta (Mokelumne)	ns	15.0	31.7	ns	0.0	0.0	ns	0.0	0.0	ns	0.0
South Delta	ns	16.0	50.6	ns	4.0	0.0	ns	0.5	0.0	ns	0.0
Upper San Joaquin River	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sacramento Valley	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[1] BP = San Francisco Bay Plankton Net Survey, 20mm = 20mm survey, SLS = Smelt Larval Survey, BOT = San Francisco Bay Study Otter Trawl, FMWT = Fall Midwater Trawl, and Kodiak Trawl = Spring Kodiak Trawl.

[2] "ns" indicates no survey conducted or regions which had inconsistently surveyed stations across all years, hence, excluded in calculating frequency of detection

later months moving downstream (Lower Rivers = July, Suisun = August, East and West Bay = September), possibly indicating downstream emigration through each Estuary area. Although LFS appeared to migrate completely out of the Lower Rivers area with an average detection frequency of zero being observed in July, monthly average detection frequencies did not drop below 2% for any Estuary area downstream.

Discussion

Observed geographic extent.—Effective conservation programs typically require a description of a species' geographical distribution or use of habitats (Pearce and Boyce 2006). Examples include reserve design (Araujo & Williams 2000), population viability analysis (Boyce et al. 1994; Akcakaya et al. 2004) and species or resource management (Johnson et al. 2004). Techniques characterizing geographical distributions by relating observed occurrence localities to environmental data have been widely applied across a range of biogeographical analyses (Guisan and Thuiller 2005). A general description of LFS distribution by occurrence was described by Moyle (2002), Rosenfield and Baxter (2007), and Rosenfield (2010); all indicated that during the LFS life cycle, it used the entire Estuary from the freshwater Sacramento-San Joaquin Delta downstream to South San Francisco Bay, and out into coastal marine waters. Regarding the extent of LFS range, those fish have been observed in a considerable portion of the western Delta, and upstream of the Feather River confluence with the Sacramento River, and the San Joaquin River to its confluence with the Tuolumne River.

Similar to the treatment of delta smelt by Merz et al. (2011), we utilized recently available data from the 20-mm and Kodiak, and Chinook and POD surveys together with other IEP and regional monitoring programs to provide information on areas of the Estuary where identified LFS life stages have been observed. While our study found similar extent of LFS distribution within the Estuary when compared with Moyle (2002), Rosenfield and Baxter (2007), and Rosenfield (2010), we observed the range of LFS extending further north on the Sacramento River, in the Petaluma River to the west, and extensions upstream on the Napa River and northern Suisun Marsh, covering an estimated area of 137,500 ha. Observations at the most upstream sampling stations in the Napa and Petaluma rivers indicated that the extent of LFS distribution in these locations remains unknown. Expanding research into these watersheds may provide insight into habitat management and future restoration for native estuarine fish assemblages including LFS (Gewant and Bollens 2012).

Distribution by life stage.— We found that LFS were frequently observed across a relatively large portion of their range, including East San Pablo Bay north into Suisun Marsh down through Grizzly Bay, and all four regions of Suisun Bay through the Confluence to the Lower Sacramento River region. Furthermore, we were able to identify regions such as Suisun Marsh and San Pablo Bay where the frequency of occurrence was relatively high in each life stage, suggesting a continuous Estuary presence. As with other anadromous species, it is likely that the mosaic of Estuary habitats provides benefits to LFS at various stages during their life history and development (Simenstad et al. 2000, Able 2005).

Identifying nursery habitats is important to conservation, as these habitats disproportionately contribute individuals to adult populations of a species (Hobbs et al. 2010). Longfin smelt are anadromous, and are known to spawn in freshwater and then move seaward for rearing. Longfin smelt have been collected in the Gulf of Farallones (Baxter

1999, CDFW 2009) and spawning has been documented in freshwater Estuary tributaries (USFWS 1996). Previous research has indicated a specific "low salinity zone" of the Estuary that serves as nursery habitat for various species (Jassby et al. 1995); in particular, the Suisun Bay has been identified as critical nursery habitat providing ideal LFS feeding and growing conditons (Hobbs et al. 2006). By utilizing all available survey data at once, we developed maps that provide evidence of a widespread rearing zone extending across the Estuary and spanning San Pablo and San Francisco bays as far upstream as the Lower Sacramento River and Lower San Joaquin River regions.

We found that both adult and larval LFS were detected relatively frequently in the uppermost regions of the Estuary (upstream of Confluence), unlike the juvenile and sub-adult life stages, likely indicating that LFS spawning habitat extends further upstream into freshwater areas than LFS rearing habitat. Unlike juvenile LFS, whose locations fluctuate between the bays and Suisun Marsh in relation to the low salinity zone (Dege and Brown 2004; Bennett et al. 2002), spawning adults appear to be not only in these locations but also to disperse into upper Delta reaches and into San Francisco Bay as well. However, adult presence in the San Francisco Bay during the spawning period likely relates to years with high Delta inflows, when low salinity habitat shifted westward. Spawning of LFS in high salinity habitat is unlikely, as such an occurrence would be maladaptive due to the low tolerance of LFS larvae to high salinity (Baxter 2009). Kimmerer et al. (2009) found larvae and juveniles most abundant at 2 ppt, and declined rapidly as salinity increased to 15 ppt.

Similar to findings of Rosenfield and Baxter (2007), we found evidence of LFS exhibiting anadromous behavior during their second year of life. The relative detection frequency of sub-adult LFS declined throughout the spring and summer months, possibly indicating a marine migration outside of the sampling area. A subsequent increase in LFS detection frequency during their second fall and winter indicates a migration back into the sampling area prior to the spring spawning season. This is consistent with an observation by Moyle (2002) that LFS gradually migrate upstream during fall and winter, as yearlings prepare for spawning. Rosenfield and Baxter (2007) also observed a decrease in LFS detection frequency and distribution after their first winter (sub-adults), followed by an increase during the second winter (adults). Although these results indicate that the marine residency of LFS is relatively brief (up to 6 to 8 months), annual variability in the duration of marine migrations remains unknown, as do the factors affecting timing of immigration and emigration (Rosenfield and Baxter 2007). There also appears to be a portion of sub-adults that do not fully leave the Estuary, suggesting a diversity in life-history strategies. A better understanding of the potential benefits of anadromy verses Estuary residency, interaction of Estuary LFS with other populations, and environmental mechanisms behind LFS anadromy appears relevant to the long-term management of this population.

Although each of the current Estuary sampling protocols suffered from one or more notable shortcomings (Bennett 2005), existing data can be explored to offer groundwork for understanding Estuary fisheries resources and specifically LFS geographic range by life stage. A better understanding of LFS spatial distribution informs conservation efforts by serving as an illustration of habitat use. Restoration strategies must include an understanding of habitat functions to effectively contribute to LFS recovery within the Estuary. There is a specific need for strategic planning in rehabilitation efforts. Some researchers have approached the question of relative influence of biological and physical factors on population abundance and the impact to conservation, and suggested mechanisms of population recovery (Mace et al. 2010). Researchers interested in developing a self-sustaining system have argued for the recovery of key processes that maintain habitat conditions (Beechie et al. 2010).

Understanding that critical differences exist in Estuary habitat value for each life stage among sites and time periods supports the use of spatial analysis in Estuary conservation and restoration planning. Exploring existing LFS data from various studies and databases, and making additional investigations into population demographics (i.e., timing or location of declines), environmental factors demonstrating the greatest influence on population abundance (e.g., temperature, water quality, prey density, etc.), and affinity analyses to assess habitat preference would provide a solid basis to address key issues. Longfin smelt are vulnerable to a large number of environmental stressors within the Estuary (Moyle 2002; Baxter et al. 2008; Healey et al. 2008) and individual stressors may have more or less significance for a species or population based on the manifestation of the stressor and proximity to that species (Tong 2001, Armor et al. 2005). Therefore, further investigations using an affinity analysis are warranted to understand more about life stage-specific key habitat attributes.

In this study, we have demonstrated the extent of LFS range is greater than previously reported (Rosenfield and Baxter 2007). We have provided additional information on distribution and detection frequencies of the Estuary population of LFS by life stage and season to support conservation planning by identifying areas to focus further study. While this analysis documents Estuary areas utilized by LFS, more work is needed to better understand the relationship between mapped spatial distribution and habitat use and productivity.

Long-term average distributional patterns are affected by inter-annual population shifts (e.g., eggs and larvae as per Dege and Brown 2004). Sampling program duration may further affect the percentage of detections at specific sites. Additionally, if the population range has shifted over time, then sampling that occurred only in recent years (e.g. in the northern Delta as the Bay Study sampling program expanded) might reveal a different pattern than if all the sampling localities in this study had been monitored over 50 years. This suggests further investigation into LFS population abundance by life stage and season is warranted, in particular investigations of the relationship between abundance and environmental factors within the Estuary.

According to Merz et al (2013), difficulty in assessing management effectiveness for anadromous fishes arises from several factors. First, anadromous life cycles are often complex and encompass both freshwater and marine ecosystems. Second, from a monitoring perspective, time series of counts at any one life stage reflect cumulative effects of freshwater, estuarine, and marine factors over the full life cycle, thereby complicating the ability to measure population responses to specific factors. Third, complex interactions of factors, which range from stream flow and temperature to large-scale and long-term shifts in marine conditions, occur. Because of these confounding factors, resource managers have not been successful in evaluating the effectiveness of managment actions that use the traditional method of quantifying abundance at single life stages in isolation. An alternative is to consider survival rates, life history variability, and the health (e.g., size, fecundity, disease) of a species that transitions between each life stage within the habitats that they occupy. Providing a spatial context for each life-stage of LFS, as we have done here, may facilitate our understanding of how Estuary habitats contribute to different life cycle stages and, thus, the effectiveness of management actions in improving population performance in the face of extrinsic constraints. Continued LFS investigations that focus on identifying, protecting, and enhancing aquatic habitats of the highest value contribute to Estuary science and management, and provide a basis for future conservation and restoration.

Acknowledgments

We gratefully acknowledge the CDFW, USFWS, and UCD, especially M. Gingras, D. Contreras, K. Hieb, J. Adib-Samii, T. Orear, R. Titus, and J. Speegle for many years of data collection and dissemination. A. Gray and K. Jones provided significant input on a previous version of this manuscript. We also thank The Fishery Foundation of California, East Bay Municipal Utility District, and CDWR for sharing data, and P. Rueger for providing assistance with GIS spatial analyses. We thank R. Baxter, J. Rosenfield, and the CFG editors, whose input was essential to the completion of this paper. Funding for this project was provided by the Center for California Water Resources Policy and Management and the State and Federal Contractors Water Agency.

Literature Cited

Able, K. 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuarine, Coastal and Shelf Science 64:5-17.

Akcakaya, H., M. Burgman, O. Kindvall, C. Wood, P. Sjogren-Gulve, J. Hatfield, and M. McCarthy. 2004. Species conservation and management. Oxford University Press, Oxford, United Kingdom.

Araujo, M., and P. Williams. 2000. Selecting areas for species persistence using occurrence data. Biological Conservation 96:331-345.

Armor, C., R. Baxter, W. Bennett, R. Breuer, M. Chotkowski, P. Coulston, D. Denton, B. Herbold, W. Kimmerer, K. Larsen, M. Nobriga, K. Rose, T. Sommer, and M. Stacey. 2005. Interagency Ecological Program synthesis of 2005 work to evaluate the pelagic organism decline (POD) in the Upper San Francisco Estuary. Interagency Ecological Program, California, USA. Available from: http://www.science.calwater.ca.gov/pdf/workshops/POD/2007_IEP-POD_synthesis_report_031408.pdf

Baxter, R. 1999. Osmeridae. Pages 179-216 *in* J. Orsi, editor. Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Interagency Ecological Program. California Department of Fish and Game, Stockton, USA. Available from: http://www.estuaryarchive.org/archive/orsi_1999/

Baxter, R., R. Breuer, L. Brown, M. Chotkowski, F. Feyrer, M. Gingras, B. Herbold, A. Mueller-Solger, M. Nobriga, T. Sommer, and K. Souza. 2008. Pelagic organism decline progress report: 2007 synthesis of results. Interagency Ecological Program Technical Report 227. California Department of Water Resources, Sacramento, USA.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. BioScience 60:209-222.

Bennett, W. A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3(2):1.

Boyce, M., J. Meyer, and L. Irwin. 1994. Habitat-based PVA for the northern spotted owl. Pages 63-85 *in* D. J. Fletcher and G. F. J. Manly, editors. Statistics in ecology and environmental monitoring. Otago Conference Series Number 2. University of Otago Press, Dunedin, New Zealand.

CDFW (California Department of Fish and Wildlife). 2009. A status review of the longfin smelt (*Spirinchus thaleichthys*) in California: report to the Fish and Game Commission. California Department of Fish and Game, Sacramento, USA. Available from: http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=10263

Chigbu, P. 1993. Trophic role of longfin smelt in Lake Washington. Ph.D. dissertation. University of Washington, Seattle, USA.

Chigbu, P. 2000. Population biology of longfin smelt and aspects of the ecology of other major planktivorous fishes in Lake Washington. Journal of Freshwater Ecology 15:543-557.

Chigbu, P. and T. H. Sibley. 1994a. Relationship between abundance, growth, egg size and fecundity in a landlocked population of longfin smelt, *Spirinchus thaleichthys*. Journal of Fish Biology 45:1-15.

Chigbu, P., and T. H. Sibley. 1994b. Diet and growth of longfin smelt and juvenile sockeye salmon in Lake Washington. Limnologie 25:2086-2091.

Chigbu, P., and T. H. Sibley. 1998. Feeding ecology of longfin smelt (*Spirinchus thaleichthys* Ayres) in Lake Washington. Fisheries Research 38:109-119.

Chigbu, P., and T. H. Sibley. 2002. Predation by longfin smelt (*Spirinchus thaleichthys*) on the mysid *Neomysis mercedis* in Lake Washington. Freshwater Biology 40:295-304.

Chigbu, P., T. H. Sibley, and D. A. Beauchamp. 1998. Abundance and distribution of *Neomysis mercedis* and a major predator, longfin smelt (*Spirinchus thaleichthys*) in LakeWashington. Hydrobiologia 386:167-182.

Clark, W. A. V. 2000. Immigration, high fertility fuel state's population growth. California Agriculture 64:8.

Dryfoos, R. L. 1965. The life history and ecology of the longfin smelt in Lake Washington. Ph.D. dissertation, University of Washington, Seattle, USA.

Eggers, D. M., N. W. Bartoo, and N. A. Rickard. 1978. The Lake Washington ecosystem: the perspective from the fish community production and forage base. Journal of the Fisheries Research Board of Canada 35:1553-1571.

Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67:277-288.

Gewant, D., and S. Bollens. 2012. Fish assemblages of interior tidal marsh channels in relation to environmental variables in the upper San Francisco Estuary. Environmental Biology of Fishes 94(2):1-17.

Graham, C. H., and R. J. Hijmans. 2006. A comparison of methods for mapping species ranges and species richness. Global Ecology and Biogeography 15:578-587.

Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Hill, I. R. 1989. Aquatic organisms and pyrethroids. Pesticide Science 27:429-465.

Healey, M. C., M. D. Dettinger, and R. B. Norgaard (editors). 2008. The State of the Bay-Delta Science 2008. CALFED Science Program, Sacramento, California, USA. Available from: http://www.science.calwater.ca.gov/publications/sbds.html

Heino, M. 1998. Management of evolving fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:1971-1982.

Hobbs, J. A., W. A. Bennett, and J. E. Burton. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Francisco Estuary. Journal of Fish Biology 69:907-922.

Hobbs, J. A., L. S. Lewis, N. Ikemiyagi, T. Sommer, and R. D. Baxter. 2010. The use of otolith strontium isotopes ($^{87}Sr/^{86}Sr$) to identify nursery habitat for a threatened estuarine fish. Environmental Biology of Fishes 89:557-569.

Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, and J. E. Cloern. 1995. Isohaline position as habitat indicator for estuarine populations. Ecological Applications 5:272-289.

Johnson, C., D. Seip, and M. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238-251.

Kimmerer, W. J. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1):1-142. jmie_sfews_10958. Available at: http://escholarship.org/uc/item/9bp499mv

Kimmerer, W. J. 2009. Individual based model for delta smelt. Presentation to National Center for Ecological Analysis and Synthesis. Pelagic Organism Decline Workshop, Santa Barbara, California, USA, September 9, 2009. Available at: http://www.cwemf.org/Asilomar/WimKimmererDeltaSmeltModel.pdf

Kimmerer, W. J., E. S. Gross, and M. L. MacWilliams. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? Estuaries and Coasts 32:375-389.

Lehman, P. W. 2004. The influence of climate on mechanistic pathways that affect lower food web production in northern San Francisco Bay Estuary. Estuaries 27:311-324.

Mace, G. M., B. Collen, R. A. Fuller, and E. H. Boakes. 2010. Population and geographic range dynamics: implications for conservation planning. Philosophical Transactions of the Royal Society B 365:3743-3751.

MacNally, R., J. R. Thomson, W. J. Kimmerer, F. Feyrer, K. B. Newman, A. Sih, W. A. Benett, L. Brown, E. Fleishman, S. D. Culberson, AND G. Castillo. 2010. Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). Ecological Applications 20:1417-1430.

Matern, S. A., P. B. Moyle, and L. Pierce. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. Transaction of the American Fisheries Society 131:797-816.

McAllister, D. E. 1963. A revision of the smelt family, Osmeridae. National Museum of Canada Bulletin 191:1-53.

Meng, L., and S. A. Matern. 2001. Native and introduced larval fishes in Suisun Marsh, California: the effects of freshwater flow. Transactions of the American Fisheries Society 130:750-765.

Merz, J. E., S. Hamilton, P. S. Bergman, and B. Cavallo. 2011. Spatial perspective for delta smelt: a summary of contemporary survey data. California Fish and Game 97:164-189.

Merz, J. E., M. Workman, D. Threloff, and B. Cavallo. 2013. Salmon life cycle considerations to guide stream management: examples from California's Central Valley. San Francisco Estuary and Watershed Science 11(2):1-26. Available from: http://escholarship.org/uc/item/30d7b0g7

Miller, J. R., and R. J. Hobbs. 2007. Habitat restoration — do we know what we're doing? Restoration Ecology 15:382-390.

Miller, W. J., B. F. J. Manley, D. D. Murphy, D. Fullerton, and R. R. Ramey. 2012. An investigation of factors affecting the decline of delta smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary. Reviews in Fisheries Science 20:1-19.

Moulton, L. L. 1974. Abundance, growth, and spawning of the longfin smelt in Lake Washington. Transactions of the American Fisheries Society 103:46-52.

Moyle, P. B. 2002. Inland fishes of California, revised and expanded. University of California Press, Berkley, USA.

Moyle, P. B., J. V. E. Katz, and R. M. Quinones. 2011. Rapid decline of California's native inland fishes: a status assessment. Biological Conservation 144:2414-2423.

Oros, D. R., and J. R. Ross. 2005. Polycyclic aromatic hydrocarbons in bivalves from the San Francisco Estuary: spatial distributions, temporal trends, and sources (1993–2001). Marine Environmental Research 60:466-488.

Pearce, J. L., and M. S. Boyce. 2006. Modeling distribution and abundance with presence-only data. Journal of Applied Ecology 43:405-412.

Rosenfield, J. A. 2010. Life history conceptual model and sub-models for longfin smelt, San Francisco Estuary population. Report for Delta Regional Ecosystem Restoration Implementation Plan. California Department of Fish and Wildlife, Sacramento, CA. Available from: https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=28421

Rosenfield, J., and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 63:683–698.

Rosenfield, J. A., and R. D. Baxter. 2007. Population dynamics and distribution patterns of longfin smelt in the San Francisco Estuary. Transactions of the American Fisheries Society 136:1577-1592.

Simenstad, C.A., W. G. Hood, R. M. Thom, D. A. Levy, and D. Bottom. 2000. Landscape structure and scale constraints on restoring estuarine wetlands for Pacific Coast juvenile fishes. Pages 597-630 *in* M. P. Weinstein and D. A. Kreeger, editors. Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, Netherlands.

Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries Magazine 32:270-277.

Thomson, J. R., W. J. Kimmerer, L. R. Brown, K. B. Newman, R. Macnally, W. A. Bennett, F. Feyrer, and E. Fleishman. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. Ecological Applications 20:1431-1448.

Tong, S. T. 2001. An integrated exploratory approach to examining the relationships of environmental stressors and fish responses. Journal of Aquatic Ecosystem Stress and Recovery 9:1-19.

USFWS (United States Fish and Wildlife Service). 1996. Sacramento-San Joaquin Delta native fishes recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, USA. Available at: http://ecos.fws.gov/docs/recovery_plans/1996/961126.pdf

van Wijngaarden, R., C. M. Brock, and P. J. Van den brink. 2005. Threshold levels for effects of insecticides in freshwater ecosystems: a review. Ecotoxicology 14:355-380.

Wang, J. C. S. 1991. Early life stages and early life history of the delta smelt, *Hypomesus transpacificus*, in the Sacramento-San Joaquin Estuary, with comparison of early life stages of the longfin smelt, *Spirinchus thaleichthys*. Technical Report 28. Interagency Ecological Program, Stockton, California, USA.

Received 8 July 2013
Accepted 21 October 2013
Associate Editor was K. Shaffer