SJC-418

American Fisheries Society Symposium 39:49–65, 2004

Effect of Outflow on Spring and Summertime Distribution and Abundance of Larval and Juvenile Fishes in the Upper San Francisco Estuary

MICHAEL DEGE

Central Valley Bay-Delta Branch, California Department of Fish and Game 4001 North Wilson Way, Stockton, California 95205-2486, USA

LARRY R. BROWN

U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, California 95819-6129, USA

Abstract.—We analyzed data on spring and summertime larval and juvenile fish distribution and abundance in the upper San Francisco Estuary (SFE), California between 1995 and 2001. The upper SFE includes the tidal freshwater areas of the Sacramento–San Joaquin Delta downstream to the euryhaline environment of San Pablo Bay. The sampling period included years with a variety of outflow conditions. Fifty taxa were collected using a larval tow net. Two common native species, delta smelt *Hypomesus transpacificus* and longfin smelt *Spirinchus thaleichthys*, and four common alien taxa, striped bass *Morone saxatilis*, threadfin shad *Dorosoma petenense*, gobies of the genus *Tridentiger*, and yellowfin goby *Acanthogobius flavimanus*, were selected for detailed analysis. Outflow conditions had a strong influence on the geographic distribution of most of the species, but distribution with respect to the 2 psu isohaline (X2) was not affected. The distribution patterns of delta smelt, longfin smelt, and striped bass were consistent with larvae moving from upstream freshwater spawning areas to downstream estuarine rearing areas. There were no obvious relationships of outflow with annual abundance indices. Our results support the idea of using X2 as an organizing principle in understanding the ecology of larval fishes in the upper SFE. Additional years of sampling will likely lead to additional insights into the early life history of upper SFE fishes.

Introduction

Fish movement and distribution patterns are governed by biotic and abiotic factors as well as behavioral or life history characteristics (Harvey 1987; Baldwin et al. 2002). Many larval fish are planktonic in their early stages and depend on hydrodynamic processes, among other factors, for dispersal into suitable rearing areas (Floyd et al. 1984; Robinson et al. 1998). The upper San Francisco Estuary (SFE) includes the tidal freshwater areas of the Sacramento–San Joaquin Delta downstream to the euryhaline environment of San Pablo Bay (Figure 1). Like other estuaries (Moyle and Cech 1999), the upper SFE provides highly productive nursery areas for many estuarine and marine fishes; however, patterns of distribution and dispersal of the larvae and early juveniles of many fishes within the estuary have not been well documented.

Declines (from early 1980s to present) have occurred in a number of upper SFE fish populations (Herbold et al. 1992; Jassby et al. 1995; Matern et al. 2002). Earlier researchers had found significant relationships between some upper SFE fishes and freshwater inflow (Turner and Chadwick 1972; Stevens 1977; Stevens and Miller 1983), although, these re-

* Corresponding author: mdege@delta.dfg.ca.gov

SJC-418

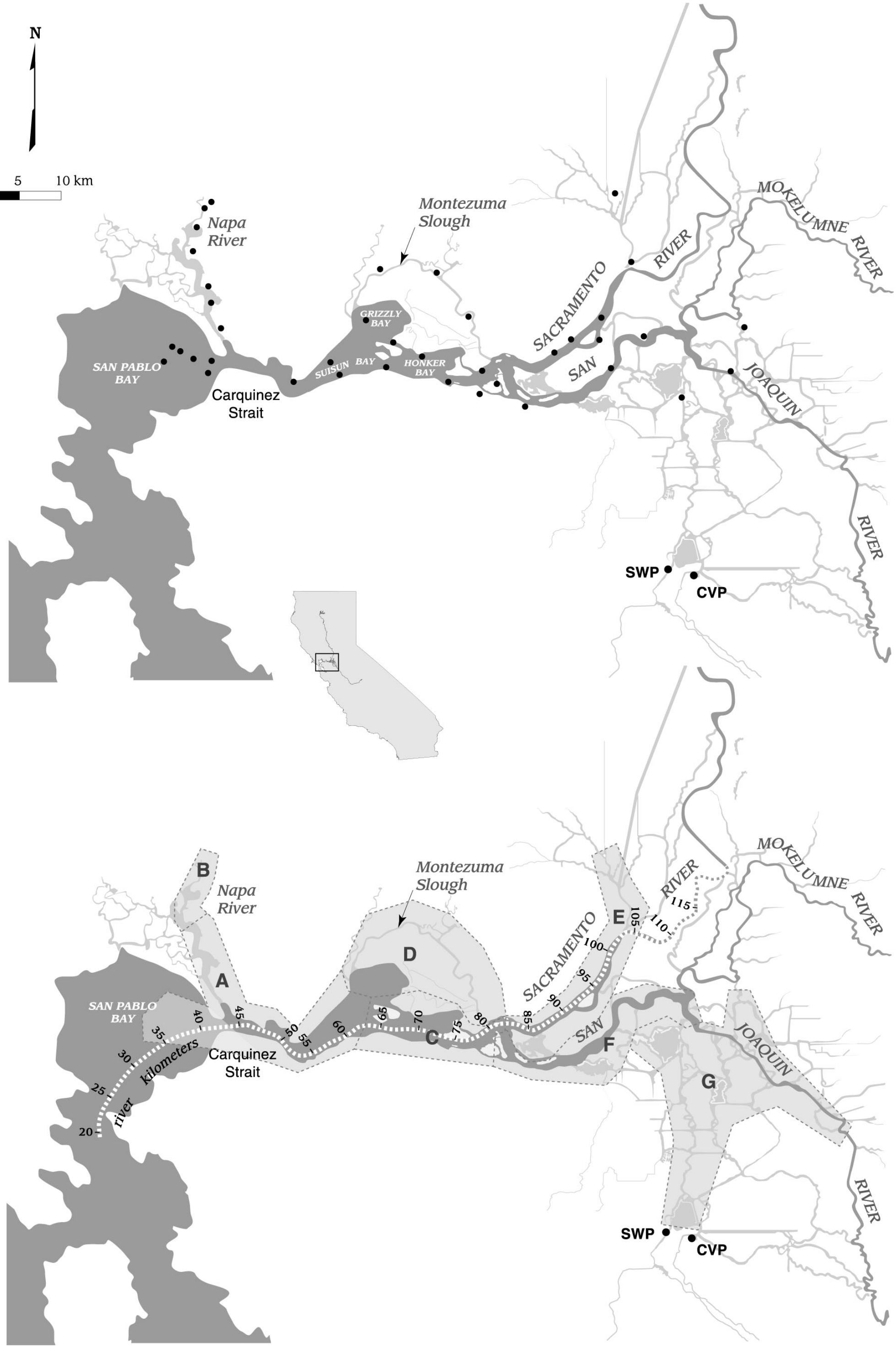

FIGURE 1. Map of the upper San Francisco Estuary showing (top panel) the 20-mm Survey sampling stations (black circles) and area groupings (bottom panel; A–G) by geographic and hydrological influence.

lationships have weakened as fish populations have declined (Kimmerer 2002a). Those studies focused on changes in freshwater inflow as the cause of fish population declines; however, numerous other changes have occurred in the SFE.

Similar to other estuaries, the SFE has been highly altered by human activities (Nichols et al. 1986). In the last 150 years, approximately 80% of tidal wetlands in San Francisco Bay have been lost, as have 95% in the delta (The Bay Institute 1998). Water management activities in the upper SFE and its tributary systems in response to increased needs for freshwater exports have been especially important in modifying the hydrology of the system (Jassby and Powell 1994; Arthur et al. 1996; Kimmerer 2002b). Further alterations include introductions of alien species (Carlton et al. 1990; Nichols et al. 1990; Alpine and Cloern 1992; Kimmerer and Orsi 1996; Greiner 2002) and changes in water quality (Nichols et al. 1986; Jassby et al. 1995; Kuivila and Foe 1995; Hornberger et al. 1999). These and other changes have likely contributed to observed declines in fish populations in the SFE (Bennett and Moyle 1996).

Environmental conditions in the upper SFE vary in response to seasonal outflow. In general, higher outflows are negatively related to electroconductivities (EC, a surrogate for salinity) and water temperatures. In the upper SFE, the position of the 2 psu isohaline (X2) is of particular interest. The X2 is measured as the distance up the axis of the estuary to the location where the daily average near-bottom salinity is 2 psu. Location of X2 in the estuary has significant statistical relationships with many estuarine resources (Jassby et al. 1995; Kimmerer 2002a, 2002b), including several species of fish. Ecological processes that generate these relationships are not well established (Kimmerer 2002b). Published studies regarding X2 have primarily focused on annual measures of X2 position and organism abundance (Jassby et al. 1995; Kimmerer 2002a, 2002b) or on detailed studies of organism behavior at or near X2 (Bennett et al. 2002; Kimmerer et al. 2002).

The objective of this study was to investigate distribution and abundance trends for fishes commonly captured by the 20-mm Survey (description follows) during the spring and summer from 1995 to 2001. Specifically, we ask the following questions:

1. How are small (<20 mm fork length [FL]) and large (≥20 mm FL) size-classes of common fishes distributed in the upper SFE both in an absolute sense (distance from the ocean) and with regard to X2 position, and how are distributions affected by outflow?
2. Are annual abundance indexes (see Methods) of the common species statistically correlated with outflow conditions or each other?

The 20-mm Survey was designed primarily to sample young-of-year delta smelt *Hypomesus transpacificus* (20 mm FL), a federal- and state-listed threatened species (Moyle 2002), throughout their historic spring and summer range. Data on the distribution and abundance of 20-mm delta smelt, along with other data, are used to evaluate the entrainment risk for delta smelt at the Central Valley Project (CVP) and State Water Project (SWP) pumping facilities located in the southern delta (Figure 1). In addition to data on delta smelt, the 20-mm Survey provides data on the larvae and juveniles of a number of other fishes utilizing the upper SFE (Table 1).

Study Area

The SFE is located in central California and encompasses an area extending from the cities of Sacramento and Stockton in the East to the Pacific Ocean in the West (Figure 1). The Sacramento and San Joaquin rivers, draining more than 40% of the state's surface area, provide the majority of freshwater to the system. These two rivers join, forming the Sacramento–San Joaquin Delta, a network of more than 1,100 km of tidal channels and sloughs (Turner and Kelley 1966). Outflow from the delta enters a series of shallow tidal bays, including the Honker, Grizzly, and Suisun bays. Outflow then enters shallow San Pablo Bay, the northernmost portion of San Francisco Bay, before reaching central San Francisco Bay and exiting to the Pacific Ocean through the Golden Gate. The upper SFE includes the region from the delta to San Pablo Bay. The cli-

TABLE 1. Common name, species name, native status, habitat, total catch, and percentage of total catch for all species captured over the study period (1995–2001) from the upper San Francisco Estuary (asterisk indicates study fish).

Common name	Species name	Native?[a]	Habitat[b]	Catch	Percent
*Longfin smelt	*Spirinchus thaleichthys*	Yes	E	289,686	36
*Gobies, *Tridentiger*	*Tridentiger* spp.	No	E	187,556	23
*Striped bass	*Morone saxatilis*	No	E, AN	95,148	12
*Yellowfin goby	*Acanthogobius flavimanus*	No	E, S	92,036	11
*Threadfin shad	*Dorosoma petenense*	No	F	55,328	7
Pacific herring	*Clupea pallasi*	Yes	S	21,103	3
*Shimofuri goby	*Tridentiger bifasciatus*	No	F, E	15,509	2
*Delta smelt		Yes	E	12,561	2
Northern anchovy	*Engraulis mordax*	Yes	S	10,376	1
White catfish	*Ameiurus catus*	No	F	8,824	1
Prickly sculpin	*Cottus asper*	Yes	E, F	6,088	<1
Channel catfish	*Ictalurus punctatus*	No	F	4,953	<1
Bay goby	*Lepidogobius lepidus*	Yes	S	4,352	<1
American shad	*Alosa sapidissima*	No	AN	1,903	<1
Threespine stickleback	*Gasterosteus aculeatus*	Yes	AN, E, F	1,411	<1
Cheekspot goby	*Ilypnus gilberti*	Yes	S	1,195	<1
Splittail	*Pogonichthys macrolepidotus*	Yes	E, F	765	<1
Starry flounder	*Platichthys stellatus*	Yes	E	686	<1
Centrarchid spp.		–	F	368	<1
Inland silverside	*Menidia beryllina*	No	E, F	255	<1
Longjaw mudsucker	*Gillichthys mirabilis*	Yes	E	239	<1
Topsmelt	*Atherinops affinis*	Yes	E, S	228	<1
White croaker	*Genyonemus lineatus*	Yes	S	221	<1
Smelt spp.		–	–	219	<1
Pacific staghorn sculpin	*Leptocottus armatus*	Yes	S	213	<1
Sacramento sucker	*Catostomus occidentalis*	Yes	F	173	<1
Common carp	*Cyprinus carpio*	No	F	124	<1
White sturgeon	*Acipenser transmontanus*	Yes	AN	120	<1
Wakasagi	*Hypomesus nipponensis*	No	E, F	113	<1
Cyprinid spp.		–	–	109	<1
Catfish spp.		–	F	88	<1
Jacksmelt	*Atherinopsis californiensis*	Yes	S	78	<1
Chinook salmon	*Oncorhynchus tshawytscha*	Yes	AN	77	<1
Plainfin midshipman	*Porichthys notatus*	Yes	S	72	<1
Bigscale logperch	*Percina macrolepida*	No	F	64	<1
Arrow goby	*Clevelandia ios*	Yes	S	60	<1
Largemouth bass	*Micropterus salmoides*	No	F	38	<1
Goby spp.		–	–	21	<1
Bluegill sunfish	*Lepomis macrochirus*	No	F	19	<1
Rainwater killifish	*Lucania parva*	No	E	17	<1
Sculpin spp.		–	–	10	<1
Tule perch	*Hysterocarpus traski*	Yes	E, F	10	<1
Bay pipefish	*Syngnathus leptorhynchus*	Yes	S	9	<1
Lampreys spp.		–	–	9	<1
River lamprey	*Lampetra ayresi*	Yes	AN	9	<1
Shokihaze goby	*Tridentiger barbatus*	No	E	9	<1
Black crappie	*Pomoxis nigromaculatus*	No	F	8	<1
Western mosquitofish	*Gambusia affinis*	No	F	7	<1
Pacific lamprey	*Lampetra tridentata*	Yes	AN	5	<1

TABLE 1. continued

Common name	Species name	Native?[1]	Habitat[2]	Catch	Percent
Goldfish	*Carassius auratus*	No	F	4	<1
Sacramento blackfish	*Orthodon microlepidotus*	Yes	F	4	<1
Speckled sanddab	*Citharichthys stigmaeus*	Yes	S	3	<1
Golden shiner	*Notemigonus crysoleucas*	No	F	2	<1
Black bullhead	*Ameiurus melas*	No	F	1	<1
Hitch	*Lavinia exilicauda*	Yes	F	1	<1
Sacramento pikeminnow	*Ptychocheilus grandis*	Yes	F	1	<1
Smallmouth bass	*Micropterus dolomieu*	No	F	1	<1
White crappie	*Pomoxis annularis*	No	F	1	<1

[a] Yes, Native; No, Alien species; –, only species are classified.
[b] Habitat: E, estuarine; AN, anadromous; F, freshwater; S, saltwater.

mate of the area is Mediterranean, characterized by mild wet winters and hot dry summers. Typically, high runoff during the winter and spring followed by low runoff during the summer and fall cause seasonal variations in salinity intrusion from the ocean.

Methods

Fish sampling

The 20-mm Survey began in 1995 and is ongoing. Based on historical records and results of other sampling programs, a network of 48 fixed sampling stations was established to encompass the historic spring and summer range of delta smelt (Figure 1). These sites also included a variety of habitats available in the system: river channels, backwater sloughs, shallow bays, and flooded islands. During the study period, sampling generally began during the first neap tidal period in early spring or when water conditions allowed the safe use of towed gear (March–April). Surveys were initiated every other week during the sampling season. Sampling continued until delta smelt larval–juvenile catch declined to low levels (i.e., a few individuals at just a few stations) and the distribution shifted such that entrainment of delta smelt at the pumping facilities located in the south delta became unlikely based on past experience (July–August). A single survey of the sampling stations usually required 6 d; however, logistical problems, such as boat or gear failures, extended some surveys into the following week. Annually, between 8 and 10 surveys were conducted.

The conical plankton net used in the surveys is 5.1 m long with a mouth opening of 1.5 m^2. The net is constructed of 1,600-µm knotless nylon delta mesh and is mounted on a weighted tow frame with skids. Fish are collected in a removable 2.2-L collection jar screened with 474-mm stainless steel wire bolting cloth. A General Oceanics flowmeter is mounted in the mouth of the net to estimate the volume (m^3) of water sampled. To sample the entire water column, three 10-min, stepped (1.2 m per step) oblique tows are completed at each station. After each tow, the entire sample is transferred to a labeled holding jar containing 10% formalin neutralized (pH 7) with sodium borate. All larval fish were identified to species or lowest possible taxon (Wang 1986) and counted. The first 300 fish (1995–1998), 100 fish (1999–2000), or 50 fish (2001) from each tow were randomly selected and measured (FL) to the nearest millimeter, except all delta smelt are measured.

Outflow conditions and X2 position

Daily outflow data were compiled from the California Department of Water Resources' (DWR) Dayflow program for the complete period of record (1955–2001; available online at http://www.iep.ca.gov/dayflow/index.html). These data were then summarized as daily averages and plotted against the daily outflow for each year of sampling (Figure 2). Years when sampling period outflow was consistently above the average for the period of record were classified as high outflow (Table 2). Years when sampling period outflow was consistently below the average were classified as low outflow (Table 2). Years when sampling period outflow was consistently near or fluctuated around the average outflow were classified as average outflow (Table 2). The most unusual year was 1997, when a major storm resulted in a record amount of outflow early in the season, but by February dry conditions prevailed (Figure 2). Location of X2 position was calculated from the DWR Dayflow program (available online at http://www.iep.ca.gov/dayflow/index.html). The X2 position represents the average daily distance (km) of X2 from the Golden Gate (i.e., Pacific Ocean).

Study fish

We restricted detailed analyses to six taxa (study fish) that we defined as common (Table 1). Common taxa were present during every year of the study and had more than 10,000 individuals in the total catch. Although many larval gobies of the genus *Tridentiger* could not be identified to species, we assume that the vast majority were shimofuri goby. The shokihaze goby is a new alien species in the system (only nine juveniles and adults collected during the study period) and has not yet become abundant (Greiner 2002). Two marine species, northern anchovy and Pacific herring were considered common, but were removed from further analysis because the upper SFE represents only a minor seasonal part of the spawning and rearing habitat for the species.

Delta smelt and longfin smelt *Spirinchus thaleichthys* are native species. The other four taxa are aliens (Dill and Cordone 1997). Striped bass was intentionally introduced into the SFE in 1879. Threadfin shad was intentionally introduced to California in 1954 and was established in the SFE by the early 1960s. *Tridentiger* spp. and yellowfin goby were not intentional introductions and likely arrived via ballast water (shimofuri goby detected in 1985, shokihaze goby detected in 1997, and yellowfin goby detected in 1963; Dill and Cordone 1997). These fishes are all pelagic (larvae only for gobies), making them susceptible to the gear.

Distribution of fishes

To account for ontogenetic changes, the common species were grouped into small and large size-classes using a 20-mm cutoff. This cutoff size was selected because it marks the transformation from the larval to the juvenile stage for most of the study fish. The gobies were exceptions because they become benthic and are less vulnerable to the net at around 15 mm. Therefore, analysis of data for gobies was limited to the smaller than 20-mm group.

For each survey, mean location of the population of each species size-class was calculated by multiplying the distance of a station from the Golden Gate (km) by the abundance (fish/10,000 m^3) of the species size-class at that site, summing across all stations, and then dividing by total abundance. We calculated distance from X2 for the population for each survey by subtracting the mean position of X2 over the time period of the survey from the weighted mean distance of X2 from the Golden Gate (km). The seven stations in the Napa River (Figure 1) were excluded from the analysis because a separate X2 develops in the Napa River Estuary independent of X2 in the upper SFE.

Weighted means (±1 SD) were plotted (not shown) and examined to determine a subset of means for analysis by repeated measures analysis of variance (ANOVA) for each species size-class. For each species size, data were examined to determine the longest series of means common to each year and outflow condition class. A series was not allowed to include gaps (surveys with no catch) or periods of widely fluctuating mean location based on few captures. Within outflow conditions, surveys from each year were selected that were approximately coincident in time (within a week). These constraints resulted in a maximum of seven surveys occurring in a data series. The selection process resulted in data series being selected for each outflow condi-

SJC-418

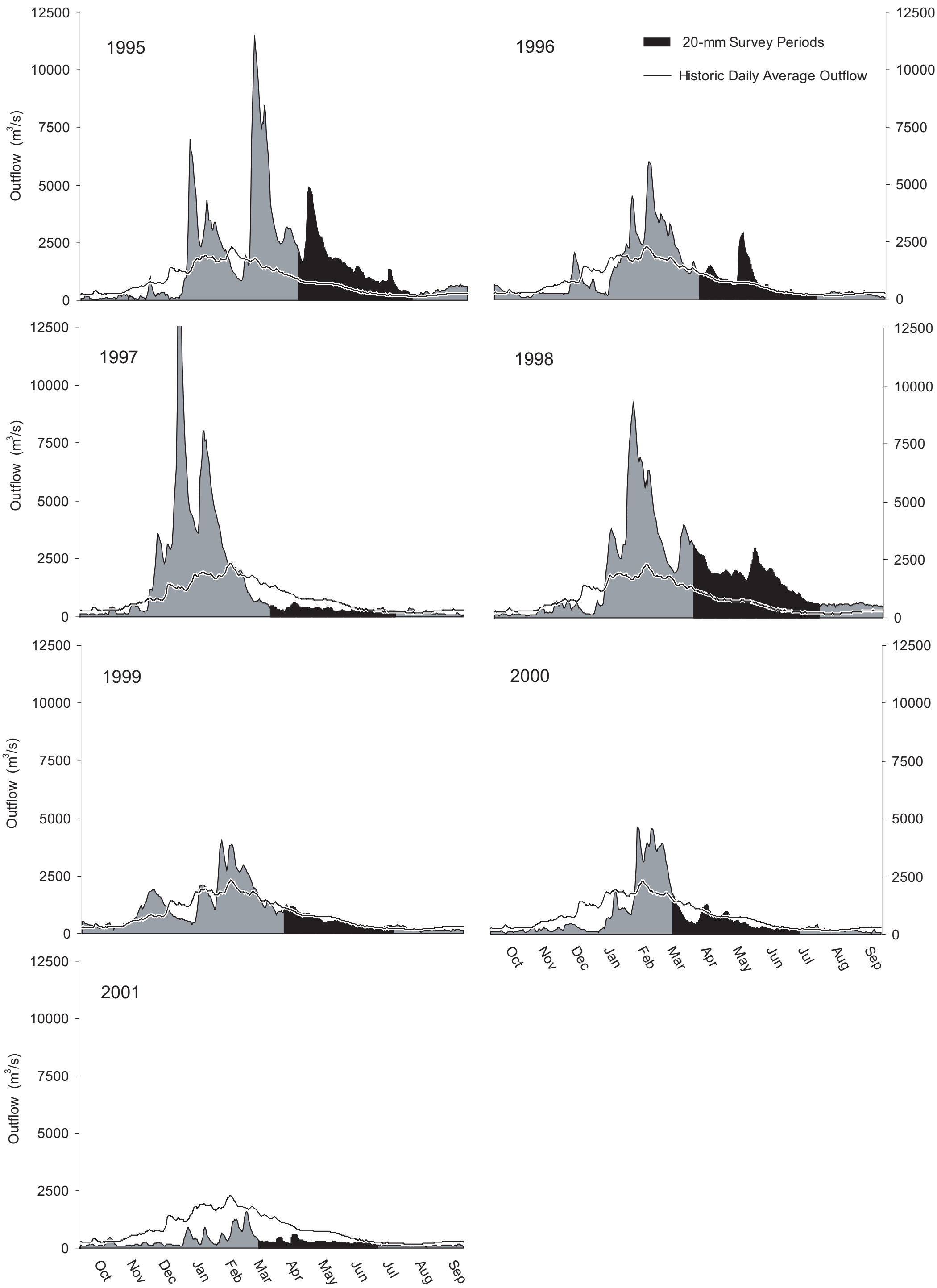

FIGURE 2. California water year (1 October–30 September) net outflow and historic (1955–2001) daily averaged net outflow through the upper San Francisco Estuary.

TABLE 2. Sampling period, average net outflow, and outflow condition classification for each year of the 20-mm Survey under investigation from the upper San Francisco Estuary.

Year	Sampling season	Average outflow (m^3/s)	Outflow condition
1995	Apr 24–Aug 8	1,546	High
1996	Apr 10–Jul 27	773	Average
1997	Mar 31–Jul 26	320	Low
1998	Apr 6–Aug 1	1,753	High
1999	Apr 12–Jul 24	558	Average
2000	Mar 20–Jul 15	566	Average
2001	Mar 19–Jul 9	269	Low

tion that might be offset by several calendar weeks from the data series for other outflow conditions for the same species size-class (see Figure 3). We assume that the series correspond to similar stages in the development of the population in response to different outflow conditions, especially for those species size-classes for which most of the surveys were included. The assumption is especially applicable to the latter portion of each series of surveys because the termination of sampling was keyed to the abundance of delta smelt. The resulting data series for distance from the Golden Gate and distance from X2 were analyzed by repeated measures ANOVA using SYSTAT 10.2 (SYSTAT Software, Inc. 2002).

As implemented in this study, the repeated measures ANOVA evaluates the main effect of outflow condition on distance from the Golden Gate and distance to X2. The analysis also tests the effect of survey number (hereinafter referred to as "time") and interactions between outflow condition and time. A significant time effect would indicate that distance changed over the series of surveys included in a data series. A significant interaction indicates that the effect of time differed between outflow conditions. For example, distance from the Golden Gate might change more rapidly at one outflow condition compared to the other two outflow conditions.

Annual abundance indices

An annual index of abundance was generated for each of the study fish. For each survey during a year, the station abundance values were multiplied by a weight factor based on an estimate of the volume of water represented by that station (Chadwick 1964). These weighted abundances were then averaged within seven geographical areas (Figure 1). These average values were then summed by survey. The final index was the sum of the values from all surveys in a year (divided by 1,000 for convenience). Associations between species and outflow conditions and among species were evaluated using Pearson's correlation coefficient (r).

Results

More than 812,000 larval and juvenile fish representing at least 24 families and 50 species were collected over the study period (some species in the families Cyprinidae, Centrarchidae, and Gobiidae are difficult to identify during the larval stage and were often grouped). Annual catches ranged from 38,856 to 340,230. The study fish accounted for 747,824 or 92% of all fishes collected (Table 1).

Distribution

Delta smelt.—Abundance at individual stations throughout the study period ranged from 0 (no catch) to 1,600 fish per 10,000 m^3. Compared to the other common fishes under investigation, delta smelt had the lowest mean abundance per station (21 fish/10,000 m^3) over the study period. Mean size of all delta smelt captured was 21.9 mm (SD = 10.2).

Small delta smelt occurred earlier and farther upstream than large delta smelt (Figures 3 and 4). This indicates that the surveys were started early in the recruitment of larvae to early juveniles. Both small and large delta smelt were generally distributed upstream of X2 (Figure 3); however, large delta smelt were centered closer to X2 than small delta smelt.

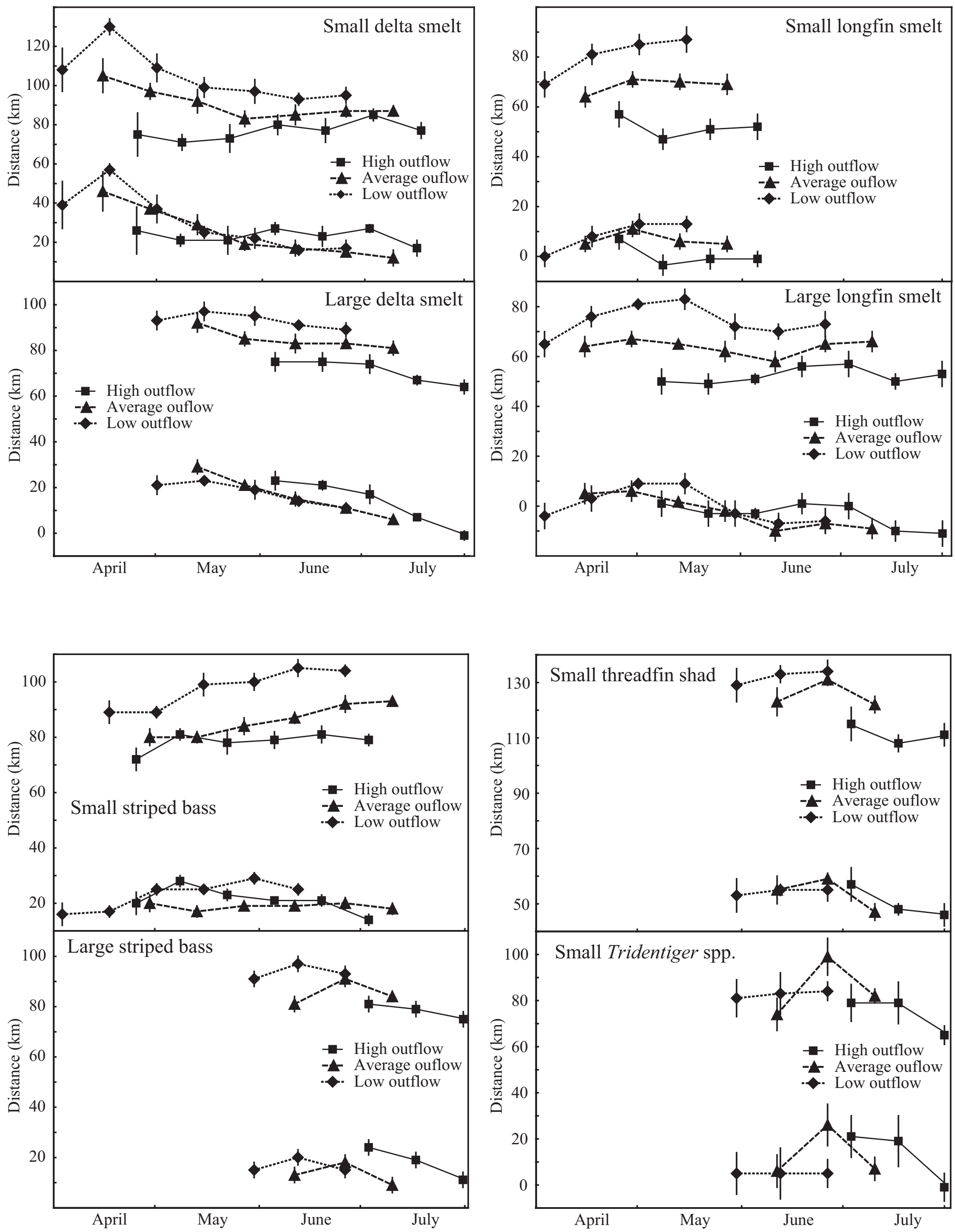

FIGURE 3. Mean (±1 SE) distance of the center of populations of small (<20 mm FL) and large (≥20 mm FL) fishes from the Golden Gate (upper three data sets) and from the position of the 2 psu isohaline (lower three data sets) for three outflow conditions. The high and low outflow conditions include 2 years of data, and the average outflow condition includes 3 years of data.

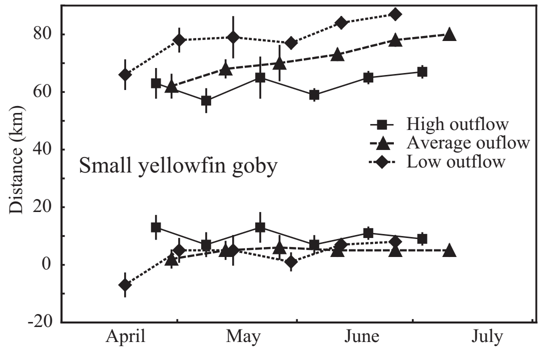

FIGURE 3. continued

These patterns are consistent with the general life history of delta smelt (Moyle 2002). Spawning occurs in freshwater with the larvae gradually moving downstream to the brackish water (1–7 parts per thousand [ppt]) habitat of juveniles and adults.

Seven survey periods were selected for quantitative analysis of small delta smelt position (Figure 3). This included most of the available data. Five survey periods were selected for quantitative analysis of large delta smelt position (Figure 3). The selection of large delta smelt data were mainly constrained by the average outflow year 1996 during which significant catches did not occur until mid-May.

Small delta smelt showed statistically significant differences among outflow conditions in distance from the Golden Gate ($F_{2,4}$ = 12.5; P = 0.019) but not for distance from X2 (P > 0.05). The population was centered closer to the Golden Gate at higher outflow; however, by the end of the sampling period, the position of the population at different outflow conditions converged (Figure 3). The mean distance from the Golden Gate at the time of the final analyzed survey was 86 km. The time trend was significant for both distance from Golden Gate ($F_{6,24}$ = 3.3; P = 0.017) and distance from X2 ($F_{6,24}$ = 8.8; P < 0.001). There was also a significant interaction of the time trend with outflow condition for both parameters ($F_{12,24}$ = 3.2; P = 0.007 and $F_{12,24}$ = 2.7; P = 0.017, respectively). The interaction can be attributed to a trend of declining distance from the Golden Gate or X2 during normal and low outflow conditions in contrast to fairly constant distances over time during high outflow conditions.

As for small delta smelt, large delta smelt showed statistically significant differences among outflow conditions in distance from the Golden Gate ($F_{2,4}$ = 12.0; P = 0.020) but not for distance from X2 (P > 0.05). Large delta smelt also tended to be centered closer to the Golden Gate during high outflow years (Figure 3). The population converged to X2 over the season, but the range in final position over the final survey period analyzed was somewhat wider than for smaller delta smelt with a mean position closer to the Golden Gate (78 km). The time trend was significant for both distance to Golden Gate ($F_{4,16}$ = 11.9; P < 0.001) and distance to X2 ($F_{4,16}$ = 46.5; P < 0.001) reflecting decreasing distances over time. The interaction between time and outflow condition was only significant for distance from X2 ($F_{8,16}$ = 2.7; P = 0.041). This likely reflects a more linear convergence of the population toward X2 during average outflow conditions compared to low and high outflow conditions (Figure 3)

Longfin smelt.—*Lo*ngfin smelt was the most common species sampled by the 20-mm Survey and was the only other native fish besides delta smelt to contribute more than 1% of the total catch over the study period (Table 1). Longfin smelt had the highest mean abundance per station over the study period of all study fish (555 fish/10,000 m^3), with abundance ranging from 0 to 90,346 fish/10,000 m^3 at individual stations. The mean size of longfin smelt captured in the 20-mm Survey was 20.2 mm (SD = 7.2).

Both small and large longfin smelt were closely associated with X2 (Figures 3). Large

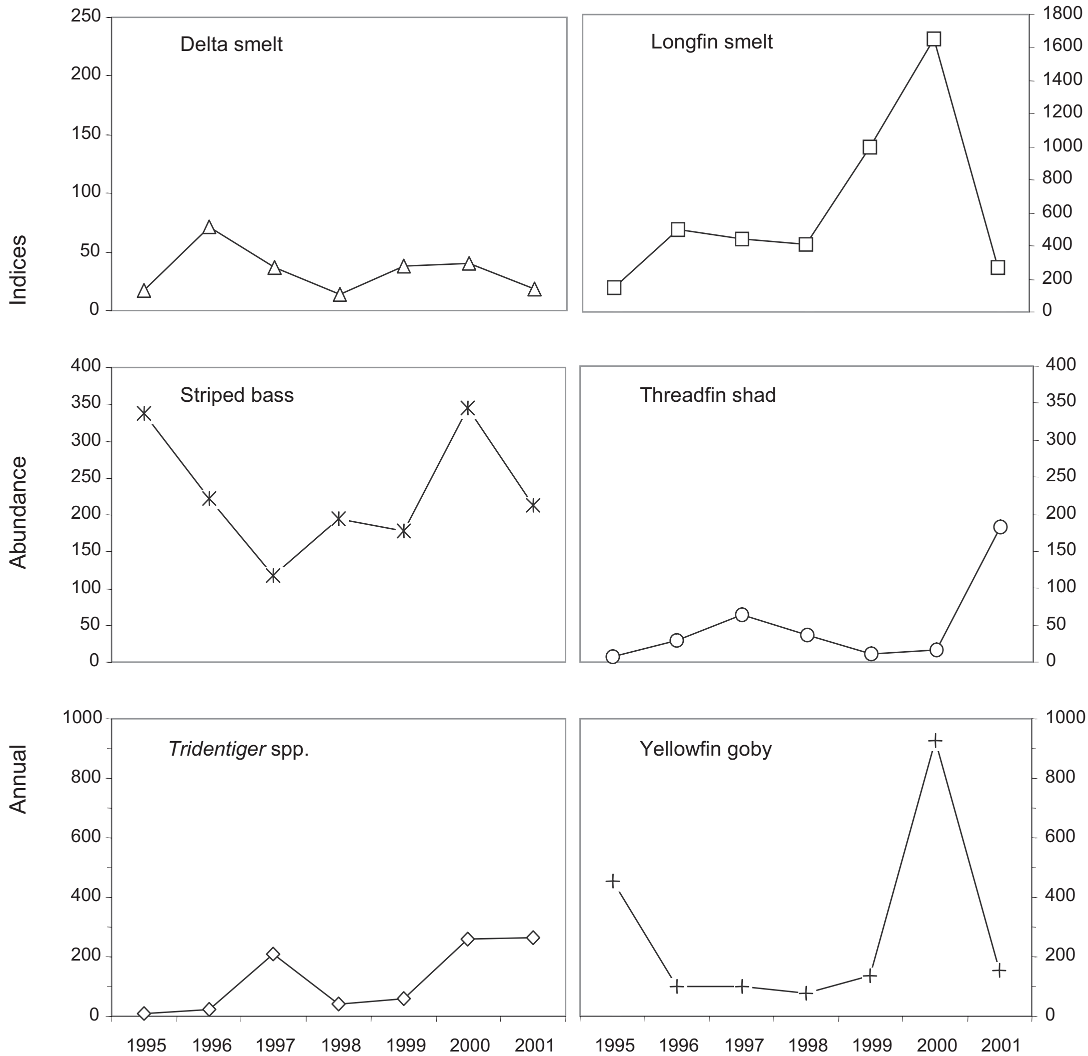

FIGURE 4. The 20-mm Survey annual abundance indices for the study fish (1995–2001).

longfin smelt were consistently found seaward of X2 during the latter part of the sampling season (Figure 3). Only four survey periods were selected for quantitative analysis of small longfin smelt position (Figure 3). The selection was mainly constrained by only sporadic catches of small longfin smelt starting in mid to late May, depending on outflow condition. Longfin smelt spawn earliest of all the study fish with most spawning taking place between January and April (Moyle 2002). Thus, the four survey periods selected likely represent the end of the reproductive season for this species. In contrast, seven survey periods were selected for quantitative analysis of large longfin smelt position (Figure 3). These periods included the majority of the available data.

There was a statistically significant difference among outflow conditions for small longfin smelt for distance to the Golden Gate ($F_{2,4} = 17.0$; $P = 0.011$) but not for distance to X2 ($P > 0.05$). As outflow increased the population was centered closer to the Golden Gate; however, the population was always closely associated with X2. For both distance to Golden Gate and distance to X2, the time trend was not significant overall ($P > 0.05$), but there was a significant interaction between the time trend and outflow condition ($F_{6,12}$ = 3.4; P = 0.034 and $F_{6,12}$ = 4.1; P = 0.017, respectively). There was not a consistent pattern among the outflow conditions. Distances increased over the four survey periods during low outflow conditions, increased and then decreased during average outflow condition, and decreased and then stayed fairly constant during high outflow conditions (Figure 3).

Large longfin smelt also showed statistically significant differences among outflow conditions for distance to the Golden Gate ($F_{2,4}$ = 38.5; P = 0.002) but not for distance to X2 (P > 0.05). As for small longfin smelt, the population was centered around X2; however, the population tended to be located seaward of X2 during the latter part of the survey period. Time was only a significant factor for distance to X2 ($F_{6,24}$ = 5.3; P = 0.001), and the interaction was not significant for either parameter (both P > 0.05). The time trend for distance to X2 was clearly indicated by the transition of the center of the population from landward to seaward of X2; however, the form of the response was not consistent among any of the outflow conditions. Longfin smelt are anadromous, and the population of late juvenile and adult longfin smelt tends to be located in San Francisco Bay (Moyle 2002), which likely accounts for the movement of the center of the population from landward to seaward of X2 during the latter part of the season.

Striped bass.—Abundance of striped bass ranged from 0 to 11,529 fish/10,000 m^3 at individual stations over the study period with a mean abundance per station of 159 fish/10,000 m^3. The mean size of striped bass captured during the study was 13.2 mm (SD = 8.2). This relatively small mean size reflects the dominance of small striped bass in the catch.

Populations of small striped bass were consistently centered upstream of X2 under all outflow conditions (Figure 3). Large striped bass also tended to occur upstream of X2; however, the population of large striped bass was centered somewhat closer to X2 than the small striped bass (Figure 3). Six survey periods were chosen for quantitative analysis of small striped bass (Figure 3). These periods included the majority of the data and were primarily constrained by sporadic catches during the early part of the surveys. Only three survey periods were selected for quantitative analysis of large striped bass (Figure 3). The main constraint was limited catches during the earlier portion of the survey period under all outflow conditions.

Distance from the Golden Gate differed significantly among outflow conditions for small striped bass ($F_{2,4}$ = 26.5; P = 0.005), but distance from X2 did not (P > 0.05). The population was centered farther upstream at lower outflows (Figure 3). The time trend was significant for distance to Golden Gate ($F_{5,20}$ = 13.7; P < 0.001) but not for distance to X2 (P > 0.05). The distance to Golden Gate tended to increase as the season progressed (Figure 3). The interaction of time with outflow condition was not significant for distance to Golden Gate (P > 0.05) but was significant for distance to X2 ($F_{10,20}$ = 4.5; P = 0.002). Through the season, the distance to X2 tended to decline at high outflow, stay constant at average outflow, and increase at low outflow (Figure 3).

Neither distance to Golden Gate nor distance to X2 exhibited statistically significant differences among outflow conditions for large striped bass (both P > 0.05). The time trend was significant for both distance to Golden Gate ($F_{2,8}$ = 27.7; P < 0.001) and distance to X2 ($F_{2,8}$ = 52.8; P < 0.001) as was the interaction of time with outflow condition ($F_{4,8}$ = 16.6; P = 0.001 and $F_{4,8}$ = 14.8; P = 0.001, respectively). The data series analyzed for large striped bass was highly constrained, and it is unclear how representative the data are for the behavior of the population. The survey period may simply not be long enough to provide a good representation of the population of large striped bass. In California, striped bass may begin spawning in April, but peak spawning occurs in May and June (Moyle 2002). Sampling, which is keyed to delta smelt abundance, may end as large striped bass are becoming abundant.

Threadfin shad.—Abundance of threadfin shad ranged from 0 to 59,374 fish/10,000 m^3 at individual stations over the study period with a mean abundance per station of 94 fish/10,000 m^3. Mean size of threadfin shad captured during the survey was 12.1 mm (SD = 5.3), reflecting the dominance of small fish in the catch.

Small threadfin shad were primarily distributed upstream of X2 (Figure 3). Except for sporadic small catches close to X2 during the earliest part of the sampling period, most threadfin shad were far upstream of X2. Sporadic catches of threadfin shad in 1999 limited quantitative analysis to three survey periods for small threadfin shad (Figure 3). Examination of the raw data suggested that these three surveys were generally representative of the behavior of the population based on years with more extensive catches. Catches of large threadfin shad were very inconsistent, especially during average outflow years, and no quantitative analysis was done for large threadfin shad. Large threadfin shad may be less vulnerable to the sampling gear because they form dense schools in contrast to the larvae, which are more dispersed (Wang 1986).

There was a significant difference among outflow periods for distance to Golden Gate ($F_{2,4}$ = 68.3; P = 0.001) but not for distance to X2 (P > 0.05). Higher outflows were associated with decreased distance to the Golden Gate. The time trend and interaction were not significant for either distance parameter (all P > 0.05).

Tridentiger spp.—Abundances of *Tridentiger* spp. ranged from 0 to 110,262 fish/10,000 m^3 at individual stations over the study period and included the highest catch per station for all of the study fish. Mean abundance per station over the study period was the second highest among the study fish at 488 fish/ 10,000 m^3. As explained in the Methods, *Tridentiger* spp. includes both *T. bifasciatus* and *T. barbatus*; however, based on juvenile and adult abundances in another SFE survey, *T. barbatus* remains rare compared to *T. bifasciatus* (Greiner 2002).

Because of sporadic catches early in the season during several years, quantitative analysis was limited to three survey periods (Figure 3). As for threadfin shad, the selection of data for analysis was constrained by limited catches early in the season in most years. Neither distance measured exhibited significant differences among outflow condition (all P > 0.05). Similarly, neither the time trend nor the interaction of time with outflow condition were statistically significant (all P > 0.05). The lack of consistent early season data are likely the result of differences in timing of spawning among outflow seasons. Moyle (2002) indicates that spawning occurs from March through August. Some catches did occur in March and April in the 20-mm Survey; however, *Tridentiger* spp. did not become a consistent part of the catch until late May (Figure 3). Thus, the sampling program may not give an accurate depiction of the mean position of the population of *Tridentiger* spp.

Yellowfin goby.—Abundances of yellowfin goby ranged from 0 to 51,985 fish/10,000 m^3 at individual stations over the study period. Mean abundance per station over the study period was 212 fish/10,000 m^3. This species tends to spawn earlier than the *Tridentiger* spp., as is evident from captures during the early portion of the survey period for all outflow conditions.

Yellowfin goby was captured consistently through the survey period, and the mean position of the population was closely associated with X2 (Figure 3). Six survey periods were selected for quantitative analysis, including the majority of the available data (Figure 3). Outflow condition and the time trend were statistically significant in the analysis of distance to Golden Gate ($F_{2,4}$ = 8.9; P = 0.034 and $F_{5,20}$ = 6.7; P = 0.001). The population was centered farther upstream during lower flows. The center of the population moved landward as the season progressed. Nothing was statistically significant in the analysis of distance to X2.

Annual abundance indices

There were few obvious patterns in the annual abundance indices (Figure 4). The correlation between annual abundance index and outflow (Table 2) was not significant for any species (all P > 0.05). The delta smelt index tended to be highest in average years. This is consistent with the hypotheses that during high outflow years (1995 and 1998) larvae are transported too far downstream and beyond shallow nursery areas (located between the confluence and Suisun Bay) and that during low outflows (1997 and 2001) the residence time of delta smelt is increased in the central and south delta where they are subjected to higher water temperatures and increased entrainment at the SWP and CVP (Moyle 2002).

However, the range in the abundance index is not particularly broad between high and low index values. Also, conclusions about high outflow years must be tentative because of the lack of data from San Pablo Bay.

Longfin smelt had some of the highest index values among the study fish (Figure 4). As with delta smelt, the highest index values occurred during average outflow years. Longfin smelt have a very strong association with X2 (Jassby et al. 1995; Kimmerer 2002a, 2002b) with the species doing very well during high outflow years. The low value for the index during high outflow years is likely due to large numbers of fish residing in San Pablo Bay where they would not be sampled by the 20-mm Survey.

The annual abundance index for striped bass had no clear associations with seasonal outflow conditions, although each low outflow season (1997 and 2001) had a lower index than the previous year (Figure 4). The annual abundance index for threadfin shad was highest during low outflow conditions (Figure 4). This was likely due to warmer temperatures being attained earlier during low outflow conditions, leading to earlier spawning and larger populations of young-of-year fish.

The annual abundance index for the gobies did not show any clear patterns. Yellowfin goby was very abundant in a high outflow year (1995) and an average outflow year (2000). *Tridentiger* spp. were most abundant in the two low outflow years (1997 and 2001) and an average year (2000).

The only significant correlation among species was between striped bass and yellowfin goby (Table 2). The significant correlation was largely due to high values for both species in 1995 and 2000. The cause for the coincidence of these high values is unknown. It is especially surprising given that yellowfin goby spawns in a more brackish area downstream of the study area (San Pablo Bay) and much of the striped bass spawning occurs upstream of the study area (Sacramento River).

Discussion

The 20-mm Survey, implemented primarily as a monitoring tool, provided significant information on the early life history of important native and alien species in the upper SFE. The results of our analyses showed that the geographic position (distance from Golden Gate) of pelagic larval and early juvenile stage fish was influenced by outflow conditions; however, no species size-class exhibited statistically significant differences in X2 position with outflow conditions. These results are consistent with studies showing that larval fishes, including striped bass, longfin smelt, yellowfin goby, and delta smelt, exhibit local vertical and horizontal migratory behaviors that tend to keep them near the low salinity zone characterized by X2 (Bennett et al. 2002). This relationship of fish populations with X2 also supports the idea that manipulating the position of X2 through water management actions will alter the position of fish populations (Kimmerer 2002b). Such manipulations may be desirable because the abundance or survival of several fishes has been linked to the position of X2 within the estuary (Jassby et al. 1995; Kimmerer 2002a), even if the specific mechanisms and processes responsible for this importance have not yet been well established (Kimmerer 2002a).

Unfortunately, the usefulness of the 20-mm Survey data were limited for some species size-classes, primarily those that did not correspond in time with high abundances of large and small delta smelt. In particular, peak abundances of large striped bass and *Tridentiger* spp. and both sizes of threadfin shad may well have occurred after the conclusion of sampling. In addition, sampling apparently started too late in the season for characterization of small longfin smelt distribution. Longfin smelt begins spawning the earliest of all of the species with most spawning occurring from February to April. Peak delta smelt spawning generally occurs in April and May (Moyle 2002).

It is interesting that the most complete data series were generally obtained for estuarine species exhibiting migratory behavior. Delta smelt, longfin smelt, and striped bass all migrate from the estuary to freshwater for spawning and the larvae then move with net outflow toward X2 (Moyle 2002). The gradual convergence of populations of small and large delta smelt on X2 (Figure 3) or slightly landward position of small and large striped bass (Figure 3) can likely be explained by patterns in upstream recruitment. The bulk of delta smelt spawning is completed during the survey period, and the bulk of the young fish have moved out of the freshwater portion of the Delta into the area of X2 by the end of sampling. Recruitment of upstream striped bass larvae likely continued for a more extended period, resulting in the center of the population being located somewhat landward of X2. Yellowfin gobies require salinities of 5 ppt or higher for successful reproduction (Wang 1986) and show a reverse migration with adults moving from Suisun Bay and other upstream areas to San Pablo Bay where salinities allow successful spawning to occur (Fleming 1999). Yellowfin goby larvae apparently move upstream into the delta using tidal currents (Wang 1986). This upstream movement was most apparent in low outflow years (Figure 3).

The annual abundance indices suggested few relationships between species and outflow conditions or between species. The lack of correlation of species abundances with outflow or among species may be real or simply an artifact of small sample size ($N = 7$). Given the complexity of the system, the factors controlling species abundances are likely numerous and interactive (Bennett and Moyle 1996), making it unlikely that such simple relationships exist. The index itself has several shortcomings. Most important, the sampling program often starts after many of the species have started spawning so many fish are missed. Further, for some species, the survey starts at different stages of the spawning season, depending on outflow conditions. Finally, any fish in San Pablo Bay, especially important during high outflow conditions, are missed. It seems unlikely that these problems will be addressed because the design of the survey is driven by logistical and safety limitations.

As in the upper SFE, studies in other areas show that estuarine species are often abundant in low salinity zones (Dodson et al. 1989; Sirois and Dodson 2000), contributing to the idea that such zones serve as important nursery areas for young fishes (Miller et al. 1985; Sirois and Dodson 2000; North and Houde 2001). The physical and behavioral mechanisms responsible for moving young fishes into estuarine nursery areas and the retention of fishes in such areas have been a main focus of research interest (Weinstein et al. 1980; Miller et al. 1985; Boehlert and Mundy 1988; Laprise and Dodson 1989a, 1989b; McGurk 1989; Sclafani et al. 1993; Bennett et al. 2002). It seems reasonable to assume that in most estuaries, the annual and seasonal development of low salinity zones and their associated biological populations would proceed on similar trajectories each year, perhaps varying in geographic position within the estuary depending on climatological factors. However, this assumption deserves examination given the ability of human water management activities, particularly diversions, to severely deplete freshwater inflows to estuaries with associated effects on biological resources (e.g., Aleem 1972; Micklin 1988). Our ability to characterize the annual and seasonal dynamics of the relationships of young fishes with a low salinity zone over an extended time period (7 years) appears to be somewhat unique in the literature. Most studies examining such relationships are limited to a few sampling periods during a few years. For example, North and Houde (2001) observed consistent relationships between fish larvae and a low salinity zone and estuarine turbidity maximum in Chesapeake Bay but only had data for a limited number of sampling periods (two or three) for 2 years. Kimmerer (2002b) examined 10 likely mechanisms for the effects of flow on biota in the SFE and found variable support for each and concluded that the effects of flow probably vary among species. In this context of ecological uncertainty combined with the high value of water in California, few assumptions remain unchallenged, and the results of our analyses will be useful in the understanding the effects of water management activities on estuarine fish populations.

Despite the difficulties with assessing annual abundance, the 20-mm Survey, designed primarily to monitor a single species, has provided valuable insights into the early life history of several ecologically important species in the upper SFE. In particular, our analyses highlighted the importance of X2 as an organizing principle for understanding larval fish ecology in the upper SFE. Additional years of sampling will surely result in new insights and better understanding of the patterns of distribution and abundance of early life stages of fish in this complex and highly modified estuary.

Acknowledgments

We would like to thank K. Fleming who provided guidance and technical support and R. Mayfield for contributions to the paper. Logistical support was provided by K. Ambrosini-Martinelli, M. Bryant, D. Crystal, K. Flowers, D. Holden, A. Holmes, N. Kalsa, L. Lynch, P. Macias, G. Schmidt, M. Silva, R. Soto, G. Webb, and S. Yuen. The Interagency Ecological Program provided program funding and oversight. The 20-mm Survey would not be possible without the numerous seasonal and scientific aides that assisted with the field as well as the laboratory components of this fast-paced and demanding monitoring program.

References

Aleem, A. A. 1972. Effect of river outflow management on marine life. Marine Biology 15:200–208.

Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946–955.

Arthur, J. F., M. D. Ball, and M. Y. Baughman. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta Estuary, California. Pages 445–495 *in* J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, San Francisco.

Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. Transactions of the American Fisheries Society 131:143–158.

Bennett, W. A., and P. B. Moyle. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin Estuary. Pages 519–542 *in* J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, San Francisco.

Bennett, W. A., W. J. Kimmerer, and J. R. Burau. 2002. Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. Limnology and Oceanography 47:1496–1507.

Boehlert, G. W., and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Pages 51–67 *in* M. P. Weinstein, editor. Larval fish and shellfish transport through inlets. American Fisheries Society, Symposium 3, Bethesda, Maryland.

Carlton, J. T., J. K. Thompson, L. E. Schemel, and F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam, *Potamocorbula amurensis.* 1. Introduction and dispersal. Marine Ecology Progress Series 66:81–94.

Chadwick, H. K. 1964. Annual abundance of young striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin Delta. California Fish and Game 50:69–99.

Dill, A. W., and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871–1996. California Department of Fish and Game, Fishery Bulletin 178, Sacramento, California.

Dodson, J. J., J. C. Dauvin, R. Ingram, and D. B. D'Anglejan. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplanktonic fauna of the middle St. Lawrence Estuary. Estuaries 12:66–81.

Fleming, K. 1999. Gobiidae. Pages 349–368 *in* J. J. Orsi, editor. Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. California Department of Water Resources, Interagency Ecological Program, Technical Report 63, Sacramento, California.

Floyd, K. B., R. D. Hoyt, and S. Timbrook. 1984. Chronology of appearance and habitat partitioning by stream larval fishes. Transactions of the American Fisheries Society 113:217–223.

Greiner, T. A. 2002. Records of the shokihaze goby, *Tridentiger barbatus* (Günther), newly introduced into the San Francisco Estuary. California Fish and Game 88:68–74.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851–855.

Herbold, B., A. D. Jassby, and P. B. Moyle. 1992. Status and trends report on aquatic resources in the San Francisco Estuary. San Francisco Estuary Project, U.S. Environmental Protection Agency, Oakland, California.

Hornberger, M. I., S. N. Luoma, A. van Geen, C. Fuller, and R. Anima. 1999. Historical trends of metals in the sediments of San Francisco Bay, California: an overview. Marine Chemistry 64:39–55.

Jassby, A. D., and T. M. Powell. 1994. Hydrodynamic influences on interannual chlorophyll variability in an estuary: upper San Francisco Bay-Delta (California, USA). Estuarine, Coastal, and Shelf Science 39:595–618.

Jassby, A. D., W. J. Kimmer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecological Applications 5:272–289.

Kimmerer, W. J. 2002a. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages. Marine Ecology Progress Series 243:39–55.

Kimmerer, W. J. 2002b. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries 25:1275–1290.

Kimmerer, W. J., J. R. Burau, and W. A. Bennett. 2002. Persistance of tidally-oriented vertical migration by zooplankton in a temperate estuary. Estuaries 25:359–371.

Kimmerer, W. J., and J. J. Orsi. 1996. Changes in the zooplankton of the San Francisco Bay Estuary since the introduction of the clam, *Potamocorbula amurensis.* Pages 403–424 *in* J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Science, San Francisco.

Kuivila, K. M., and C. G. Foe. 1995. Concentrations, transport and biological effects of dormant spray pesticides in the San Francisco Estuary, California. Environmental Toxicology and Chemistry 14:1141–1150.

Laprise, R., and J. J. Dodson. 1989a. Ontogenetic changes in the longitudinal distribution of two species of larval fish in a turbid well-mixed estuary. Journal of Fish Biology 35(Supplement A):39–47.

Laprise, R., and J. J. Dodson. 1989b. Ontogeny and importance of tidal vertical migrations in the retention of larval smelt *Osmerus mordax* in a well-mixed estuary. Marine Ecology Progress Series 55:101–111.

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

McGurk, M. D. 1989. Advection, diffusion and mortality of Pacific herring larvae, *Clupea harengus pallasi*, in Bamfield Inlet, British Columbia. Marine Ecology Progress Series 51:1–18.

Micklin, P. P. 1988. Desiccation of the Aral Sea: a water management disaster in the Soviet Union. Science 241:1170–1176.

Miller, J. M., L. B. Crowder, and M. L. Moser. 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. Contributions to Marine Science 27:338–352.

Moyle, P. B. 2002. Inland fishes of California. Revised and expanded. University of California Press, Berkeley.

Moyle, P. B., and J. J. Cech, Jr. 1999. Fishes: an introduction to ichthyology, 4th edition. Prentice Hall, Englewood Cliffs, New Jersey.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. Science 231:567–573.

Nichols. F. H., J. K. Thompson, and L. E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam, *Potamocorbula amurensis*. 2. Displacement of a former community. Marine Ecology Progress Series 66:95–101.

North, E. W., and E. D. Houde. 2001. Retention of white perch and striped bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. Estuaries 24:756–769.

Robinson, A. T., R. W. Clarkson, and R. E. Forrest. 1998. Dispersal of larval fishes in a regulated river tributary. Transactions of the American Fisheries Society 127:772–786.

Sclafani, M. C., C. T. Taggart, and K. R. Thompson. 1993. Condition, bouyancy and the distribution of larval fish: implications for vertical migration and retention. Journal of Plankton Research 15:413–435.

Sirois, P., and J. J. Dodson. 2000. Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt, *Osmerus mordax*. Marine Ecology Progress Series 203:233–245.

Stevens, D. E. 1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 106:34–42.

Stevens, D. E., and L. W. Miller. 1983. Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin River system. North American Journal of Fisheries Management 3:425–437.

SYSTAT Software, Inc. 2002. SYSTAT 10.2, Statistics I. SYSTAT Software, Inc. Richmond, California.

The Bay Institute. 1998. From the Sierra to the sea. The Bay Institute of San Francisco, San Rafael, California.

Turner, J. L., and H. K. Chadwick. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 101:442–452.

Turner, J. L., and D. W. Kelley. 1966. Ecological studies of the Sacramento-San Joaquin Delta, Part II, fishes of the delta. California Department of Fish and Game, Fish Bulletin 136, Sacramento, California.

Wang, J. C. S. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: a guide to their early life histories. California Department of Water Resources, Interagency Ecological Program, Technical Report 9, Sacramento, California.

Weinstein, M. P., S. L. Weiss, R. G. Hodson, and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. U.S. Fishery Bulletin 78:419–436.