

Fish 56

Effects of River Flow on Abundance of Young Chinook Salmon, American Shad, Longfin Smelt, and Delta Smelt in the Sacramento-San Joaquin River System

DONALD E. STEVENS AND LEE W. MILLER

California Department of Fish and Game
Bay-Delta Fishery Project
4001 North Wilson Way
Stockton, California 95205

This peer-reviewed article contains a statistical error that vitiates its findings about the effects of Delta inflows on juvenile Chinook salmon (error masked by use of an index).

ABSTRACT

Annual abundance indices for young fall-run chinook salmon (*Oncorhynchus tshawytscha*), American shad (*Alosa sapidissima*), and longfin smelt (*Spirinchus thaleichthys*) increased directly with river flow rates during the spawning and nursery periods. Annual abundance of young delta smelt (*Hypomesus transpacificus*) did not vary with river flow. Several factors associated with flow could explain the relationships described for chinook salmon, American shad, and longfin smelt. The one factor common to all affected species was that dispersal of young increases when flows increase, which probably results in decreased density-dependent mortality.

Water development in the Sacramento-San Joaquin River system has modified the magnitude and pattern of river flows, and these alterations have affected fish production (Stevens and Chadwick 1979). Survival of young striped bass (*Morone saxatilis*) and subsequent recruitment have been reduced due to water projects altering flows during and shortly after spawning (Turner and Chadwick 1972, Stevens 1977a, Chadwick et al. 1977). Also, salmon runs in the San Joaquin drainage have been severely depleted since the construction of dams on the spawning tributaries. At present, the numbers of San Joaquin River chinook spawners are highly correlated ($r = 0.83$ for the period 1960-1976) with flow rates from March to June when they were outmigrants 2½ years earlier (California Department of Fish and Game 1976).

To increase our understanding of water project impacts on young chinook salmon (*Oncorhynchus tshawytscha*) and three other anadromous species—American shad (*Alosa sapidissima*), longfin smelt (*Spirinchus thaleichthys*), and delta smelt (*Hypomesus transpacificus*)—we calculated annual abundance indices for each species and examined their relationship to river flows.

As human needs for water increase, knowledge of flow requirements becomes essential if we are to maintain adequate instream flows for fish (Orsborn and Allman 1976). Such knowledge of striped bass requirements has recently been used

by the California State Water Resources Control Board in adopting appropriate flow standards and placing operational constraints on the U.S. Bureau of Reclamation's Central Valley Project (CVP) and California's State Water Project (SWP) (Stevens 1980).

STUDY AREA

The Sacramento River and San Joaquin River are the major streams in California's Central Valley (Fig. 1). Their drainage basin is about 153,000 km². These rivers form a tidal estuary extending from their junction in the delta to the Golden Gate at the entrance of San Francisco Bay. The historical annual flow from the rivers averaged about 1,100 m³/second but now only about one-half that amount passes through the estuary due to local use along the rivers and exports to the San Joaquin Valley and Southern California (Chadwick 1977). Seasonal flow patterns have been modified by water storage in upstream reservoirs in winter and spring with subsequent release for diversion in summer and fall. Diversions by the CVP and SWP averaged 190 m³/second in 1978 and could increase to about 270 m³/second in 25 years under present authorizations (Chadwick 1977). The CVP and SWP pumping plants are in the southern Delta. Roughly 85% of the water that they export originates in the Sacramento River, 10% is from the

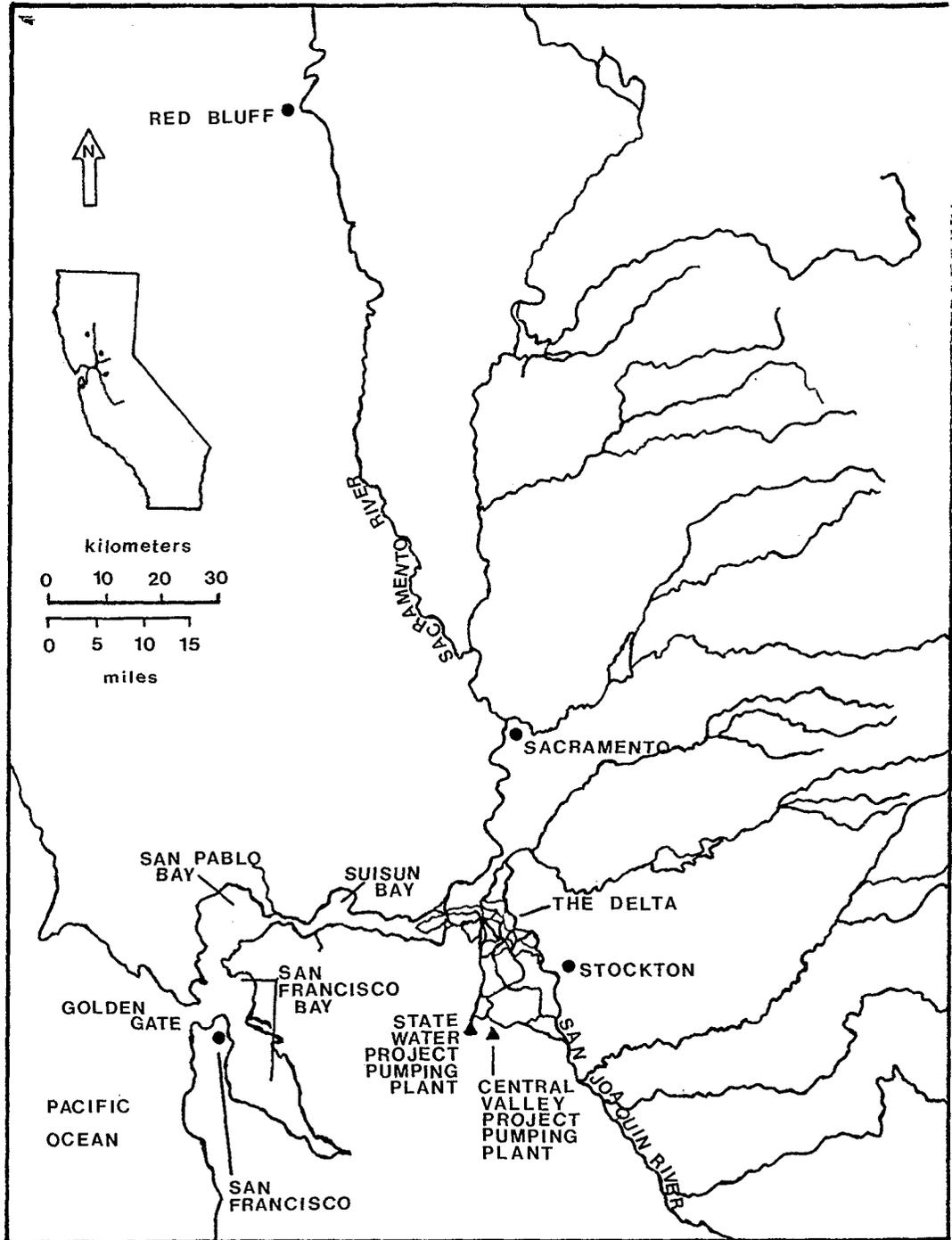


Figure 1. The Sacramento-San Joaquin river system.

San Joaquin River, and 5% is from miscellaneous eastern valley streams.

LIFE HISTORY RESUMÉS

Chinook Salmon

More than 90% of the chinook salmon in the Central Valley spawn in the Sacramento River and its tributaries upstream from the Delta. The remainder spawn in the San Joaquin system. There are four major runs in the Sacramento River system: fall, late fall, winter, and spring. The fall-run is the largest numerically, comprising about 80% of the stock (Kjelson et al. 1982). In the San Joaquin system the salmon are almost all fall-run fish. The run to which individual smolts belong cannot be positively identified, because spawning and migration periods of the various runs overlap. However, the fall-run probably was the primary group indexed because it is the most numerous stock and it migrates to the ocean during the months that we sampled. Nevertheless, some fish from the other runs certainly were included.

Fall-run salmon spawn from mid-October through December (Taylor 1976) and hatching occurs 50–60 days after spawning. The young emerge from the redds about 3–4 weeks later. Smolts that average about 8 cm fork length (FL) migrate through the estuary on their way to the ocean primarily from April through June (Sasaki 1966), although in years with high winter and spring runoff many smaller young enter the estuary a few days after emerging (Kjelson et al. 1981). Also, some young remain in the upper river throughout the summer and migrate in the fall. These older migrants often exceed 10 cm FL (Schaffter 1980).

American Shad

American shad were introduced into the estuary in 1871 and rapidly became abundant (Fry 1973). Shad spawn in both the Sacramento and San Joaquin River systems but, like chinook salmon, the major runs are in the Sacramento River and its tributaries. The upstream migration starts in March; spawning occurs from April to June and peaks in late May or June; the eggs drift near the bottom; and they hatch in 4–6 days. The young migrate seaward through the estuary from June to December (Stevens 1966a).

Longfin Smelt

Adult longfin smelt migrate from salt and brackish water to the Delta during winter. Spawning occurs in the Delta from December through April (Simonsen 1977). The eggs probably adhere to the river bottom (Fry 1973) but the larvae are pelagic. Young longfin smelt usually are abundant in the Delta, Suisun Bay, and San Pablo Bay from spring through fall.

Delta Smelt

Like the longfin smelt, adult delta smelt begin migrating to the Delta during the winter. However, delta smelt spawn later than longfin smelt, primarily from April through June, and the young tend to concentrate in the Delta and Suisun Bay.

METHODS

The importance of river flow to the various species was examined by (1) calculating abundance indices for each species, and (2) computing correlation coefficients between the abundance indices and averages of daily river flow rates for various combinations of months during the spawning and nursery periods. Although we hypothesized that flow might affect year-class strength, we did not know in advance which month or combination of months would be important to the various species. Hence, we tested flows from all possible combinations of successive months between spawning and the start of the periods for which we measured abundance (Fig. 2). The use of many combinations of months and the fact that flows in successive months are interrelated substantially increases the probability of obtaining spurious, statistically significant correlations. Therefore, we present the correlations primarily as a guide to interpreting which periods are important.

Data from the California Department of Water Resources on total inflow to the Delta were used to index the flow. Studies of geographical distributions of chinook salmon (Sasaki 1966, Taylor 1976), American shad (Stevens 1966a), and smelt (Radtke 1966) in the Sacramento-San Joaquin system lead us to believe that spawners are distributed roughly in proportion to flow from the rivers; thus "total inflow" should reflect general conditions in the spawning and nursery areas.

Regression models were developed for the periods with the best abundance-flow correlations

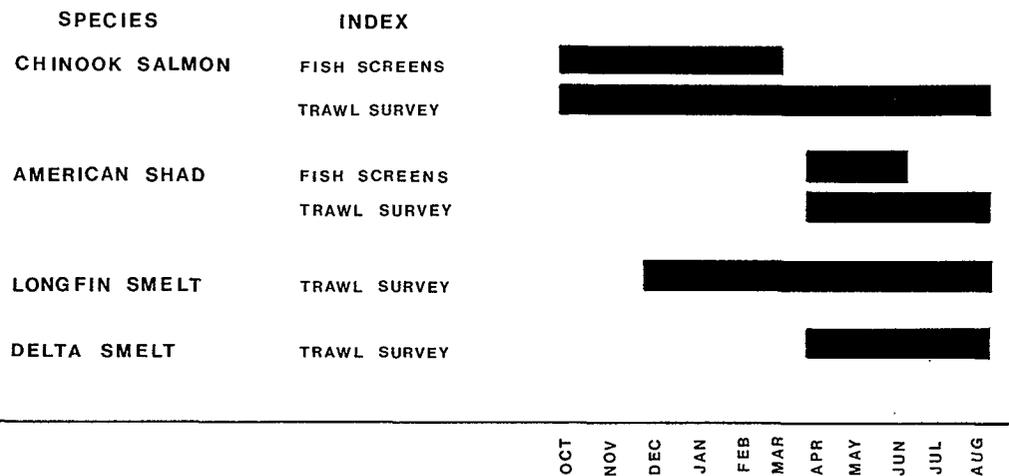


Figure 2. Months included in evaluations of flow effects on abundance indices of four species of fish in the Sacramento-San Joaquin river system. Data were acquired at fish screens and by midwater trawls.

to provide a basis for predicting year-class strength.

DEVELOPMENT OF ABUNDANCE INDICES

We used two methods to index chinook salmon and American shad and one method to index the smelts. The abundance indices were log-normally distributed so they were transformed to \log_{10} before statistical analysis.

Midwater Trawl Index

Abundance of all four species was indexed from annual midwater trawl surveys conducted monthly from September to December 1967-1978 (1974 not surveyed). These surveys were designed principally to measure striped bass abundance but catches of chinook salmon, American shad, and smelt were recorded. Except when inclement weather or other problems prevented sampling, each monthly survey consisted of one 12-minute, depth-integrated tow at each of 87 sampling stations scattered from San Pablo Bay through the Delta (Stevens 1977b). The trawl was 17.6 m long with a mouth opening 3.7 m square. It was constructed of nine tapered panels with mesh sizes ranging from 14.7 cm stretch mesh at the mouth to 1.3 cm stretch mesh at the

cod end. The net was towed at about 0.1 m/second. This net was most efficient for fish <10 cm long. Hydrofoils, depressor doors, and mode of operation were similar to those described by Von Geldern (1972).

Monthly abundance indices were calculated for each species by: (1) dividing the survey area into 17 regions; (2) multiplying the mean catch of each species at the stations within each region by the water volume estimated by the California Department of Water Resources to be in each region; and (3) summing those products. We use the sums of those monthly abundance indices in our analysis.

Fish Screen Index

The second method of indexing abundance of chinook salmon and American shad was based on estimated catches of young migrants at the louver fish screens in front of the CVP and SWI pumping plants in the southern Delta. These pumping plants are on a normal migration route for fish from the San Joaquin but not the Sacramento River (Fig. 1). However, the Sacramento River is the primary source of water for the CVP and SWP, and many fish from that drainage probably are drafted to the pumps with the cross

delta flow of Sacramento River water. The screens, their operation, methods of sampling, and estimation of catch were described by Skinner (1974).

This index (N_t) was calculated using the equation $N_t = C_t \div D_t$, where C_t = estimated catch during time t and D_t = the fraction of delta inflow diverted by the CVP and SWP during time t . C_t 's were estimated by expanding complete counts of fish guided into a holding tank during sampling periods that varied in duration from about 15 seconds every 2 hours when fish were abundant to the entire period when fish were scarce.

The sampling schedule resulted in at least an 80% chance that the estimates represented the true catch $\pm 100\%$ (Bay-Delta Fishery Project 1981). Often, sampling was more intensive and the resulting estimates were more precise, but confidence intervals were not routinely calculated.

Data were available to calculate annual N_t 's for chinook salmon using total April through June catches from 1959 to 1979 (no 1963 data available). The annual American shad index was based on catches from July through September 1959-1979.

The N_t indices underestimated abundance because screening efficiency was less than 100% (Skinner 1974), and there is a high mortality of fish in the vicinity of the diversions (Schaffter 1978, Hall 1980) which probably caused the fraction of the run that was screened to be less than the fraction of Delta inflow that was diverted. However, N_t is a valid index if the fraction of the run screened is proportional to the fraction of the inflow that is diverted.

Assessment of Index Reliability

Various factors such as annual differences in the relative abundance of fish in the Sacramento and San Joaquin drainages and the timing of their migrations cause our indices to be imprecise. However, having two independent indices for both chinook salmon and American shad provided an opportunity for comparisons to aid assessment of their reliability. Similar trends would suggest that both indices were dependable. Thus, correlation analyses were used to evaluate the extent to which the trends agreed. We believe that these correlations (presented later in this report) and the general similarity among the correlations between abundance and flow based on the two index types indicate that both indices

Table 1. April-June total catches of young chinook salmon at the Central Valley and State Water Project fish screens, the fraction of Delta inflow diverted in April-June, and two indices of abundance.^a

Year	Total catch	Fraction diverted	Screen index $\times 10^4$	Trawl index $\times 10^4$
1959	71,436	0.238	30	
1960	61,608	0.181	34	
1961	65,616	0.222	30	
1962	92,400	0.127	73	
1963				
1964	127,944	0.236	54	
1965	326,552	0.065	502	
1966	106,968	0.206	52	
1967	49,380	0.023	215	46
1968	135,121	0.349	39	93
1969	98,622	0.044	224	152
1970	408,003	0.268	152	140
1971	418,992	0.137	306	74
1972	340,466	0.405	84	49
1973	201,350	0.254	79	72
1974	254,193	0.113	225	
1975	121,637	0.147	83	19
1976	90,494	0.371	24	35
1977	12,783	0.217	6	4
1978	41,120	0.105	39	44
1979	202,123	0.306	66	

^a Screen index = catch \div fraction of inflow diverted.

are reliable enough to identify major differences in abundance.

RESULTS

Chinook Salmon

Annual abundance indices based on the fall trawl survey varied greatly, with the highest index (1969) being almost 40 times greater than the lowest index (1977). The index of young salmon abundance based on catches at the CVP-SWP fish screens in the spring fluctuated even more than the index based on the trawl survey. It ranged from about 60,000 fish in 1977 to more than 5 million fish in 1965 (Table 1).

The correlation between the logarithms of the two indices ($r = 0.75$) was imprecise but statistically significant ($P < 0.01$) (Fig. 3). Both indices for 1977, a drought year, were exceptionally low and they obviously swayed this correlation. The imprecision in these results could reflect annual differences in relative abundance of spring and fall outmigrants and/or error associated with both measures of abundance. Hence, the indices probably disclosed major trends, but they might not reveal moderate differences in abundance.

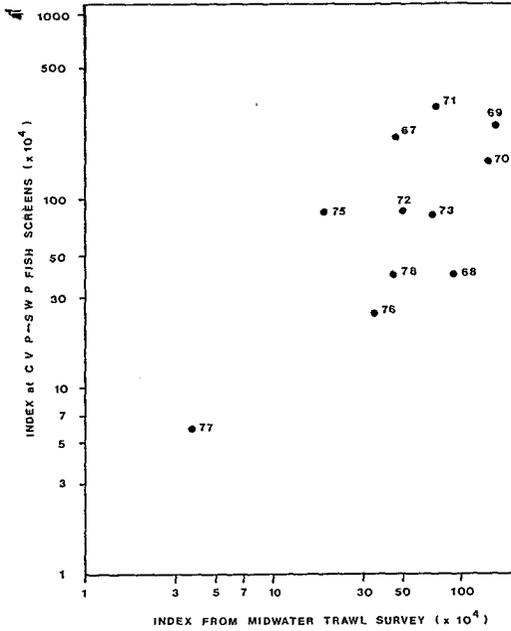


Figure 3. Correlation of 0.75 between two indices of young chinook salmon abundance. Numbers adjacent to data points indicate year of data collection. (CVP-SWP = Central Valley Project-State Water Project)

Correlations between the salmon abundance index based on the fall midwater trawl survey results and river flow were statistically significant for 34 of the 60 combinations of months tested

(Table 2). The trawl data indicated that survival of young salmon was influenced most by flow during January. None of the correlations that included only the months before January and only two after January were statistically significant—February alone and February–March. However, the highest correlation coefficient (0.71) was between the abundance index and the mean flows for October through February.

The regression equation that best predicted the trawl-based index was: \log_{10} salmon abundance index = $1.03 + 0.00057 \times$ mean October–February inflow to the Delta ($m^3/second$). The regression accounted for 57% of the variation in the index.

Using the abundance index based on catches at the CVP-SWP fish screens, 18 of the 21 correlation coefficients describing the relation between chinook salmon abundance and various combinations of monthly flow from October–March were statistically significant ($P < 0.05$) (Table 3). In contrast to the trawl data which indicated that January was the most important month, the fish-screen index indicated that December flows were the most critical. The correlations not significant were for the three periods before December. The highest correlation coefficient (0.81) was between abundance and December flow and coefficients for combinations of months that included December were all greater than coefficients for combinations of months without December.

December flows alone provided the highest correlation coefficient; therefore, they provide t

Table 2. Correlation coefficients between \log_{10} index of young chinook salmon abundance (measured by midwater trawl surveys) and inflow to the Sacramento-San Joaquin Delta, 1967–1974 (no data for 1974). Coefficients are for the entire period between corresponding months on the two axes. For example, 0.40 is the correlation coefficient between abundance and mean flow for all months from March to June.^a

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Oct	0.23										
Nov	0.27	0.29									
Dec	0.40	0.39	0.38								
Jan	0.71*	0.71*	0.70*	0.67*							
Feb	0.76**	0.74**	0.74**	0.70*	0.67*						
Mar	0.75**	0.74**	0.73*	0.70*	0.64*	0.53					
Apr	0.73*	0.72*	0.71*	0.68*	0.59	0.46	0.31				
May	0.70*	0.69*	0.68*	0.65*	0.55	0.42	0.30	0.28			
Jun	0.68*	0.66*	0.66*	0.63*	0.53	0.40	0.30	0.29	0.28		
Jul	0.67*	0.66*	0.65*	0.64*	0.52	0.40	0.30	0.30	0.30	0.34	
Aug	0.68*	0.66*	0.65*	0.63*	0.53	0.41	0.33	0.33	0.36	0.46	0.5

^a * $P < 0.05$, ** $P < 0.01$.

Table 3. Correlation coefficients between \log_{10} index of young chinook salmon abundance (based on catches at Central Valley and State Water Project fish screens) and inflow to the Sacramento-San Joaquin Delta, 1959-1979 (no data for 1963). Coefficients are for the entire period between corresponding months on the two axes. For example, 0.79 is the correlation coefficient between abundance and mean flow for all months from November to January.^a

	Oct	Nov	Dec	Jan	Feb	Mar
Oct	0.14					
Nov	0.34	0.38				
Dec	0.73**	0.76**	0.81**			
Jan	0.78**	0.79**	0.80**	0.68**		
Feb	0.78**	0.80**	0.80**	0.68**	0.53*	
Mar	0.78**	0.78**	0.77**	0.66**	0.53*	0.46*

^a * $P < 0.05$, ** $P < 0.01$.

best basis for predicting the index. The regression equation is: \log_{10} salmon abundance index = $5.38 + 0.0048 \times$ December inflow to the Delta in m^3/second . This equation accounted for 65% of the variation in the index.

American Shad

Catches of American shad during the mid-water trawl survey indicated that abundance varied by a factor of 16.6 from 1967 to 1978. This index was lowest in 1976 and highest in 1969. American shad indices derived from catches at the CVP-SWP fish screens varied by a factor greater than 100 from 1959 to 1979. The low index was about 490,000 fish in 1976 (Table 4); the highest was 69.6 million fish in 1967. The next highest index, 7.6 million fish in 1975, was roughly one order of magnitude less than the 1967 index.

The exceptionally high index at the CVP-SWP screens in 1967 caused the 1967 data point to not conform to the plot of the other years. Nevertheless, the correlation between the two indices was statistically significant ($P < 0.01$) suggesting that both indices reasonably measured spawning success (Fig. 4).

Correlations between indices obtained by trawling and flow were statistically significant for all 15 combinations of months from April through August (Table 5). The highest correlation coefficient was for April; however, it was only slightly higher than the coefficient for May and also those for several other combinations of months. In

Table 4. July-September total catches of young American shad at the Central Valley and State Water Project fish screens, the fraction of Delta inflow diverted in July-September, and two indices of abundance.^a

Year	Total catch	Fraction diverted	Screen index $\times 10^4$	Trawl index $\times 10^4$
1959	155,618	0.255	61	
1960	107,604	0.297	36	
1961	226,704	0.317	72	
1962	245,822	0.260	95	
1963	788,900	0.218	362	
1964	225,957	0.276	82	
1965	1,112,940	0.325	342	
1966	491,710	0.289	170	
1967	9,118,990	0.131	6,961	3,460
1968	642,387	0.364	176	760
1969	672,565	0.158	426	5,660
1970	161,662	0.240	67	950
1971	491,787	0.231	213	2,100
1972	386,280	0.366	106	500
1973	349,592	0.385	91	1,040
1974	1,998,279	0.314	636	
1975	2,492,912	0.325	767	2,490
1976	223,673	0.455	49	340
1977	207,481	0.165	126	650
1978	1,287,855	0.418	308	3,310
1979	408,250	0.541	75	

^a Screen index = catch \div fraction of inflow diverted.

general, the coefficients decreased as flows from the later months were included. The April regression equation accounted for 86% of the variation in the index. This equation is: \log_{10} shad abundance index = $2.62 + 0.00051 \times$ April inflow to the Delta (m^3/second).

The indices based on catches at the fish screens were significantly correlated with all combinations of monthly flows from April to June. However, the results differed from those based on the trawl survey in that April appeared to be the least important month. The coefficients ranged from 0.73 for the April flow to 0.86 for the June and average May-June flows (Table 6). The May-June regression equation (\log_{10} shad index = $5.59 + 0.00093 \times$ mean May-June inflow to the Delta [m^3/second]) provided the best predictions. It described 74% of the variation in the index.

Longfin Smelt

Our annual measurements of longfin smelt abundance varied substantially. Abundance in 1967, the peak year, was more than 450 times greater than in 1977, the lowest year (Table 7).

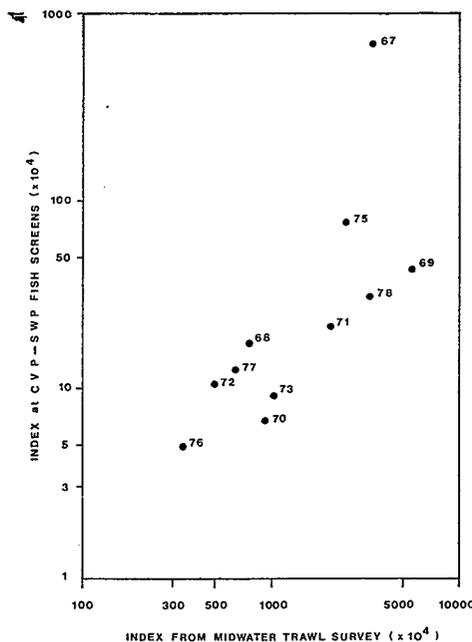


Figure 4. Correlation of 0.73 between two indices of young American shad abundance. Numbers adjacent to data points indicate year of data collection. (CVP-SWP = Central Valley Project-State Water Project)

Correlations between longfin smelt abundance and flow were statistically significant ($P < 0.05$) for 43 of the 45 combinations of months from December to the following August (Table 8). The

Table 5. Correlation coefficients between \log_{10} index of young American shad abundance (measured by midwater trawl survey) and inflow to the Sacramento-San Joaquin Delta, 1967-1978 (no data for 1974). Coefficients are for the entire period between corresponding months on the two axes. For example, 0.90 is the correlation coefficient between abundance and mean flow for all months from April to August.^a

	Apr	May	Jun	Jul	Aug
Apr	0.93**				
May	0.92**	0.89**			
Jun	0.90**	0.86**	0.79**		
Jul	0.89**	0.85**	0.79**	0.72*	
Aug	0.90**	0.86**	0.81**	0.76**	0.68*

^a * $P < 0.05$, ** $P < 0.01$.

Table 6. Correlation coefficients between \log_{10} index of young American shad abundance (based on catches at Central Valley and State Water Project fish screens) and inflow to the Sacramento-San Joaquin Delta, 1959-1979. Coefficients are for the entire period between corresponding months on the two axes. For example, 0.85 is the correlation coefficient between abundance and mean flow for all months from April to June. All coefficients are significant at $P < 0.01$.

	Apr	May	Jun
Apr	0.72		
May	0.80	0.83	
Jun	0.85	0.86	0.86

only correlations not statistically significant were those for the single months of December and January. The highest correlation coefficients (0.93) were for the mean monthly flow over the entire periods of December-July and December-August. Looking at individual months, correlation coefficients for April, May, June, and July were somewhat greater than that for August and those for the months before April. These results, then, suggest that longfin smelt survival has been controlled primarily by spring and early-summer flows. Eighty-six percent of the variation in the longfin smelt abundance index is accounted for by the equation: \log_{10} longfin smelt index = $2.18 + 0.0014 \times$ mean December-August inflow to the Delta ($m^3/second$).

Delta Smelt

Annual abundance of delta smelt varied by only a factor of 5.3. Lowest abundance was in

Table 7. Indices of smelt abundance ($\times 10^4$) in the Sacramento-San Joaquin Estuary, as measured by a midwater trawl survey.

Year	Longfin smelt	Delta smelt
1967	84,504	414
1968	3,422	690
1969	59,563	315
1970	8,011	1,679
1971	16,189	1,298
1972	528	1,375
1973	5,914	1,145
1975	2,794	682
1976	751	435
1977	187	505
1978	6,666	656

Table 8. Correlation coefficients between \log_{10} index of longfin smelt abundance (measured by midwater trawl survey) and inflow to the Sacramento-San Joaquin Delta, 1967-1978 (no data for 1974). Coefficients are for the entire period between corresponding months on the two axes. For example, 0.90 is the correlation coefficient between abundance and mean flow for all months from January through July.^a

	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Dec	0.56								
Jan	0.68*	0.58							
Feb	0.76**	0.69*	0.76**						
Mar	0.80**	0.73*	0.77**	0.70*					
Apr	0.86**	0.81**	0.85**	0.83**	0.84**				
May	0.90**	0.86**	0.88*	0.85**	0.84**	0.84**			
Jun	0.92**	0.89**	0.90**	0.88**	0.86**	0.85**	0.84**		
Jul	0.93**	0.90**	0.91**	0.88**	0.86**	0.86**	0.84**	0.82**	
Aug	0.93**	0.90**	0.91**	0.89**	0.87**	0.87**	0.86**	0.83**	0.71*

^a * $P < 0.05$, ** $P < 0.01$.

1969; the highest in 1970 (Table 7). There were no statistically significant ($P \leq 0.05$) correlations between the delta smelt abundance indices and combinations of monthly flows from the start of spawning in April until August—the last month before our survey began (Table 9). Notably, all of the correlation coefficients except the one for August were negative, which is contrary to expectations based on correlations between abundance and flow for the other species. We did not develop a regression model for delta smelt because all of the correlations between their abundance and flow were nonsignificant.

DISCUSSION

The abundance of young chinook salmon, American shad, and longfin smelt increased with

Table 9. Correlation coefficients between \log_{10} index of delta smelt abundance (measured by midwater trawl survey) and inflow to the Sacramento-San Joaquin Delta, 1967-1978 (no data for 1974). Coefficients are for the entire period between corresponding months on the two axes. For example, -0.33 is the correlation coefficient between abundance and mean flow for all months from June to August. None of the coefficients is significant at $P < 0.05$.

	Apr	May	Jun	Jul	Aug
Apr	-0.45				
May	-0.48	-0.51			
Jun	-0.48	-0.49	-0.46		
Jul	-0.46	-0.46	-0.39	-0.16	
Aug	-0.44	-0.42	-0.33	-0.04	0.14

river flow during the spawning and/or nursery months. We found no significant correlations between abundance of delta smelt and river flows, and those relationships generally were inverse. Hence, the delta smelt results are at odds with the other results. Although the delta smelt's life history is similar to that of longfin smelt, the delta smelt's abundance apparently is not determined by the same factors because its population remained relatively stable over a wide range of flows.

The salmon, shad, and longfin smelt results were similar in that abundance was significantly correlated with flow during many monthly periods. Some of these statistically significant relationships may not be biologically significant because monthly flows tend to be interrelated.

The periods that appeared to be most important for salmon and shad differed for the analyses based on the trawl survey and those based on catches at the fish screens. However, these inconsistencies were relatively minor as the highest correlations for the different data sets were within the same general seasons.

We examined several potential explanations for the different results obtained with the two sets of chinook salmon and American shad indices.

Chinook Salmon:

- (1) Salmon caught at the screens migrated several months earlier and therefore may have been spawned earlier than those caught by the trawl. The salmon caught at the screens also were more highly correlated with earlier flows; thus, if the two indices represent dif-

- ferent runs or portions of runs, the results may reflect the same flow-related mechanisms operating during different time periods.
- (2) Releases of hatchery-reared salmon could affect the two indices differently. However, the impact of these releases is virtually impossible to evaluate because hatchery-raised salmon are released at various stages of development and at many locations which causes the timing of their migrations and their survival to vary (Kjelson et al. 1982).
 - (3) The data for fish screens extended over more years than the trawling data; therefore, the results could have differed due to a shift in the critical period. On the other hand, correlations using the fish-screen index only from 1967 to 1978 (except 1974), the years with both data sets, were essentially the same as over the entire series of years (1959-1979). The correlation for December ($r = 0.75$) was still higher than the correlation for January ($r = 0.60$). Hence, this explanation was rejected.
 - (4) The inconsistencies simply could be caused by imprecision in the indices due to variability associated with sampling intensity and annual differences in fish distribution, their migration routes, and the timing of their migrations.

American Shad:

- (1) The different results did not reflect identical mechanisms affecting early and late runs because the screen index was based on earlier migrants, yet it was more highly correlated with the later flows.
- (2) As for salmon, there was no evidence that the critical period had shifted. Correlations using the fish-screen index only from the years with both data sets did not change results appreciably. The correlations for June ($r = 0.87$) and May-June ($r = 0.87$) were still higher than the correlation for April ($r = 0.79$).
- (3) The most probable explanation is that the results have been affected by imprecision in the data. The shad indices are affected by the same sampling and behavioral factors potentially causing variability in the salmon indices.

The importance of river flow is not limited to those periods that we have defined. For example,

we found that winter flows probably influence survival of young salmon; yet, salmon spawning runs in the San Joaquin system are correlated with river flows during the March-June smolt outmigration 2½ years earlier (California Department of Fish and Game 1976). During the outmigration, operators of storage dams often severely reduce flows allowing water temperatures to become lethal in that drainage. It is also noteworthy that summer streamflow apparently affects survival of young coho salmon (*Oncorhynchus kisutch*) in the Puget Sound region (Mathews and Olson 1980).

We have identified five factors that are potentially responsible for the high correlations between fish abundance and flow that we have documented for the Sacramento-San Joaquin system. The possible importance of these factors varies among the species:

- (1) Extended periods of redd dewatering are known to increase mortality of chinook salmon eggs, embryos, and alevins (Bauersfeld 1978, Becker et al. 1982). In the Sacramento and San Joaquin rivers, redd dewatering occurs after salmon spawn in shallow areas of the river bed during short-term rises in water level following storms (R. E. Painter, R. J. Hallock, California Department of Fish and Game, personal communications). Some chinook salmon spawning takes place throughout the year (Taylor 1976); therefore, dewatering potentially is a mortality factor in all months although storms come primarily from about November to April. Redd dewatering is the most probable flow-related factor that could have caused the fish-screen index to closely correlate with December flow. Most of the largest chinook run, the fall-run, spawn by December and their eggs are incubating then. The ratio of December flow (incubation): mean October-November flow (spawning) in the Sacramento River above Bend Bridge near Red Bluff (California Department of Water Resources) should crudely index dewatering. The correlation coefficient between the salmon index based on catches at the fish screens and this ratio is 0.77 ($P < 0.01$) and is consistent with, but does not confirm, the dewatering hypothesis.
- (2) As flows decrease, losses of fish increase at the CVP and SWP diversions in the Delta, and also at several thousand, mostly un-

screened, small irrigation diversions located throughout the Sacramento and San Joaquin river systems. Losses increase because these diversions remove fairly constant amounts of water each year so that the percentage of flow and fish that are diverted varies inversely with flow rate. Such losses partly explain the relationship between young striped bass abundance and flow (Chadwick et al. 1977) and, except for salmon, could explain many of the correlations that we have described. Chinook salmon are an exception because relatively little water is diverted from the areas that most salmon inhabit during the months that seem to be most important.

- (3) Predation on young fish may increase during low flow years because the water tends to be clearer and the young are more concentrated in smaller river volumes. Squawfish (*Ptychocheilus grandis*) are significant predators on salmon (Hall 1979), and striped bass are major predators on the young of virtually all fishes in the river system (Stevens 1966b, Thomas 1967, Hall 1980).
- (4) High flows increase habitat availability which may improve survival of young fish by reducing intraspecific competition. We have observed, but not documented, that when flows are high there is increased use of Sacramento River tributaries by adult chinook salmon and American shad for spawning; consequently, nursery habitat increases for their young. Furthermore, sampling with nets has demonstrated that high flows disperse young salmon (Kjelson et al. 1982), shad, and smelt (unpublished data) throughout the rivers and estuary. Increased dispersal of young also helps explain the striped bass abundance-flow relationship (Stevens 1977a, Chadwick et al. 1977).
- (5) Biologists studying the Sacramento-San Joaquin Estuary (Turner and Chadwick 1972) and other systems (George 1972; Sutcliffe 1972, 1973) have suggested that nutrients that form the base of food chains increase with flow, thereby increasing production in the fisheries. Although this process may contribute to the striped bass relationship (Turner and Chadwick 1972, Chadwick et al. 1977), it apparently is not the major factor (Chadwick et al. 1977). Probably it can be eliminated as a cause of the salmon and shad correlations but not for the longfin smelt.

During the first several months of life, the major nurseries of salmon and shad lie upstream where, due to different hydraulic conditions, nutrients are less likely to vary with flow than in the estuary.

Regressions provide estimates of how much the abundance of each species is affected by river flow, but the various factors affecting the precision of the data, our inability to detect specific critical periods due to the interrelation of monthly flows, and other factors that probably create bounds to fish production all affect this quantification. Nevertheless, we present these estimates to provide a general sense of the flow effects within the limits of our data. The regressions based on the screening and trawling data indicated chinook salmon abundance increased about 12% for every 100 m³/second of daily mean December flow and 7% for each 100 m³/second of daily mean October-February flow, respectively. The corresponding regressions for American shad indicated increases of 23% per 100 m³/second of daily mean May-June flow and 12% per 100 m³/second of daily mean April flow. Longfin smelt abundance increased by increments of 38% for each 100 m³/second of daily mean December-August flow.

From a practical management standpoint, the value of the correlations that we have described would be enhanced if they were based on numbers of recruits entering the fisheries or if numbers of recruits could be related to abundance at the stages we have monitored. Available data are not adequate for these evaluations. However, it is reasonable to presume such relationships exist. They have been described for various fish populations including Sacramento-San Joaquin striped bass (Stevens 1977a) and San Joaquin chinook salmon (California Department of Fish and Game 1976).

In summary, our analysis and previous work on striped bass and salmon indicate that survival of the young of several species of fish in the Sacramento-San Joaquin river system improves as river flow increases during and/or shortly after the spawning seasons. Several factors may be responsible, with their relative importance varying among species. The apparent general effect of high flow on all of the species is to increase the quality and quantity of nursery habitat and more widely disperse the young fish, thus reducing density-dependent mortality.

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