Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages?

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ABSTRACT: All ecosystems are influenced by physical forcing. Estuarine ecosystems respond most strongly on an interannual timescale to variability in freshwater flow. Several mechanisms for positive or negative flow effects on biological populations in estuaries have been proposed; however, positive effects appear to operate mainly through stimulation of primary production with effects propagating up the food web. In the northern San Francisco Estuary, abundance or survival of several common species of fish and shrimp varied positively with flow-in data through 1992. I re-examined these relationships and those of several additional taxa in an analysis of long-term (20 to 40 yr) monitoring data. The spread of the introduced clam Potamocorbula amurensis in 1987 provided an opportunity to examine simultaneously the responses of estuarine species to flow and to changes in the food web. I separated variability into a flow response, a step change after 1987 and other sources of variability. Responses of fish and shrimp contrasted with those of lower trophic levels. All but 1 species of nekton responded positively to flow, only 2 had clear declines after 1987, and none of the relationships changed in slope after 1987. In contrast with the higher trophic levels, chlorophyll a (chl a) and several species of zooplankton declined markedly after 1987, and had either weak responses to flow or responses that changed after 1987. Thus, the food web appears strongly coupled between benthos and plankton, and weakly coupled between zooplankton and fish, as has been found in other systems. More importantly, the variation with freshwater flow of abundance or survival of organisms in higher trophic levels apparently did not occur through upward trophic transfer, since a similar relationship was lacking in most of the data on lower trophic levels. Rather, this variation may occur through attributes of physical habitat that vary with flow.

KEY WORDS: Estuary · Food web · Freshwater flow · Salinity · Introduced species

INTRODUCTION

Estuarine ecosystems provide goods and services with high economic value (Costanza et al. 1997) including significant fisheries (Houde & Rutherford 1993). They are subject to substantial alteration by humans (Nichols et al. 1986) and they may play a significant role in the global carbon balance (Smith & Hollibaugh 1993). Much of the high temporal and spatial variability in physical, chemical and biological conditions in estuaries occurs through seasonal and interannual variability in freshwater flow (Skreslet 1986). River discharge into many estuaries is substantially altered by diversion for human use and may be sensitive to climate change (Vörösmarty et al. 2000). Thus, understanding mechanisms by which estuarine ecosystems respond to freshwater flow should yield important insights into the dynamics of these key ecosystems as well as their sensitivity to human intervention and climate variability.

Numerous examples exist in which estuarine populations or communities vary with freshwater flow. Pos-
itive flow effects have been reported for phytoplankton production (Riley 1937, Cloern et al. 1983, Ingram et al. 1985, Malone et al. 1988, Gallegos et al. 1992, Mallin et al. 1993, Sin et al. 1999), and abundance or harvest of benthic invertebrates (Aleem 1972, Gammelsrød 1992, Montagna & Kalke 1992, Wilber 1992, 1994) and fish (Stevens 1977, Houde & Rutherford 1993, Jassby et al. 1995). Negative effects on biological populations can also occur, e.g. through effects of washout or osmotic stress (Deegan 1990, Kaartvedt & Aksnes 1992), or combinations of effects (Howarth et al. 2000). Rose & Summers (1992) found instances of positive, negative and no effects of freshwater flow on estuarine fish populations.

Estuarine populations may respond to increasing freshwater flow through several alternative mechanisms (Drinkwater & Frank 1994). Increased nutrient loading may stimulate phytoplankton production (Riley 1937) according to the ‘agricultural model’ (Nixon et al. 1986), which may apply in many estuaries (e.g. De Jonge et al. 1994). Sutcliffe (1972, 1973) proposed that increased freshwater flow and nutrient loading stimulated phytoplankton production, increasing fishery yield. Sutcliffe’s argument was disputed by Drinkwater & Myers (1987) on statistical grounds and by Sinclair et al. (1986) on the basis of interpretation, but the concept has persisted. Phytoplankton blooms can also be stimulated through haline stratification, which may be correlated with freshwater flow (e.g. Cloern 1991).

To explain flow effects on animal populations, both the agricultural model and the stratification model require trophic transfer up the food web. Aquatic ecosystems including estuaries may show stronger food-web dynamics than terrestrial systems (Polis 1999). However, estuarine systems are also open and strongly influenced by physical variability, which may obscure food-web effects. Furthermore, the concept of ‘bottom-up’ regulation oversimplifies the responses of real aquatic food webs to stimulation at their base (e.g. McQueen et al. 1989, Micheli 1999).

Numerous environmental attributes may covary (positively or negatively) with freshwater flow and contribute to mechanisms for population responses to flow. Examples include: (1) flow patterns in the watershed and freshwater reach, such as flooding of river margins and proportion of freshwater diverted for human use; (2) changes in loading or dilution of materials from the watershed including nutrients, organic matter, sediments, contaminants and planktonic organisms; (3) physical changes in the estuary including the movement and compression of the estuarine salt field, stratification, residual circulation and residence time; and (4) changes in the hydrodynamic environment, such as the location and amplitude of maxima in turbidity, and chemical and biological constituents of the estuary (Postma 1967, Jassby et al. 1993, 1995, Monismith et al. 1996, 2002). Because this list is so long, statistical analyses may fail to distinguish among alternative mechanisms underlying any particular relationship with flow. Nevertheless, such analyses can be helpful in eliminating possible mechanisms.

In this paper, I examine long-term (20 to 40 yr) monitoring data from the San Francisco Estuary to determine modes of variability related to flow and those related to long-term changes in the food web. The San Francisco Estuary is a large, strongly tidal, heavily modified estuary with a residence time on the order of months (Walters et al. 1985). Most of the historic fringing marsh has been eliminated (Nichols et al. 1986) and most of the organic carbon supply to the open water is from phytoplankton (Jassby et al. 1993, Canuel et al. 1995, Jassby & Cloern 2000). The emphasis in this paper is on the northern estuary (San Pablo Bay to the western Sacramento-San Joaquin Delta, Fig. 1), the region of greatest variability due to freshwater flow. A suite of estuarine-dependent pelagic species has been selected for analysis including all those discussed by Jassby et al. (1995). I have added several fish species, the abundant copepod Acartia spp. and rotifers, and chlorophyll a concentration in 2 salinity ranges. The species included in the analysis are mostly abundant estuarine-dependent species present for the duration of the monitoring programs and have contrasting life history patterns, including several anadromous fish species and a number that spawn in the ocean or the lower estuary and move up the estuary as young (see Table 1).

Some relationships of population attributes to flow in the San Francisco Estuary have been reported before. Flow was once a good predictor of abundance of striped bass young-of-year (YOY) (Turner & Chadwick 1972) and recruitment (Stevens 1977) indices, although declines in the spawning stock appear to have reduced that predictive capacity (Kimmerer et al. 2001). Abundance of the bay shrimp Crangon franciscorum (Hatfield 1985) and young of several fish species (Stevens & Miller 1983) varied with freshwater flow. Jassby et al. (1995) presented relationships of abundance of a few estuarine-dependent species to a salinity variable called X2, which is the horizontal distance up the axis of the estuary to where tidally averaged near-bottom salinity is 2 psu, i.e. roughly the center of the low salinity zone (LSZ, defined as salinity of 0.5 to 6 psu). This variable reflects the physical response of the estuary to changes in flow and provides a geographic frame of reference for estuarine conditions. Salinity between 2 and about 30 psu is roughly linearly distributed between X2 and the mouth of the estuary (Monismith et al. 1996).
An inadvertent experiment provided a glimpse into the trophic processes in the estuarine pelagic food web. The introduced clam Potamocorbula amurensis spread throughout San Pablo and Suisun Bays and into the western Delta in 1987, reducing chl a along with abundance of larger phytoplankton and some zooplankton later that year and into subsequent years (Alpine & Cloern 1992, Kimmerer & Orsi 1996, Orsi & Mecum 1996, Lehman 2000). Adding 7 to 8 yr of data after this event to those analyzed by Jassby et al. (1995) allowed for a contrast between food-web and flow effects. The flow responses reported by Jassby et al. (1995) could have arisen through stimulation at the base of the food web or through direct physical effects. If the responses to flow were due to food-web effects, we would expect 2 conditions to be true: (1) either positive or trophically alternating responses should be seen in the lower as well as higher trophic levels; and (2) changes in the flow responses due to the loss of phytoplankton biomass after 1987 should be similar at lower and higher trophic levels. I show here that the responses of lower and higher trophic levels were qualitatively different, implying that mechanisms for the responses of fish and shrimp to flow were not due to effects of flow on the base of the food web.

Jassby et al. (2002) detected 2 modes of variability in chl a and primary production in the Delta (see Fig. 1). The first was a long-term decline in summer chl a concentrations, which they attributed to the grazing by Potamocorbula amurensis. The second was a winter-spring mode that varied inversely with flow and had a long-term decline of unknown cause. Analyses presented here focus on spring-summer, when the fish and shrimp are in larval and juvenile stages, and on salinity above 0.5 psu. This implies some overlap with the data used by Jassby et al. (2002), although as shown below, the patterns of variability were somewhat different.

**METHODS**

Sources of data and the methods used to calculate X2 were explained in detail by Jassby et al. (1995) and are described only briefly here. Daily values of X2, the distance up the axis of the estuary to where daily average near-bottom salinity is 2 psu, were calculated from 1968 to 1992 by interpolation among fixed salinity monitoring stations. For other years, X2 was calculated from time series regression relating X2 to the previous day’s X2 and the log of the current day’s net freshwater flow into the estuary, which is calculated from gauged flows and estimated net consumption in the Delta (California Department of Water Resources unpubl. data). Values used were means over 1 or more months, so errors in freshwater flow estimates had at most a minor effect on the X2 values. Error variance for the estimation of daily X2 values was ~2 km² (Jassby et al. 1995). Variance of seasonally averaged X2 values was ~100 km²; therefore, X2 can be treated as if measured without error. The averaging period for X2 differed among species: it was based generally on the larval development periods of the fish and shrimp (Jassby et al. 1995) or for planktonic species, the months during which samples were taken.

Data to develop biological response variables were obtained from the database of the Interagency Ecological Program for the San Francisco Estuary (IEP; www.iep.water.ca.gov), a consortium of state and federal agencies that runs several estuarine monitoring programs. Response variables included chl a, abundance of several planktonic taxa, and annual indices of abundance or survival of several species of fish and shrimp (Tables 1 & 2). These monitoring programs have used consistent methods since their inception, although the number and distributions of stations have changed in some cases. All response variables were log-transformed to homogenize error variance, with constants added in some cases to account for 0 catches in the data.

Data for lower trophic levels were obtained from IEP monitoring programs that focus on Suisun Bay and the Delta, with at most 2 stations in San Pablo Bay (Fig. 1). Zooplankton abundance data were obtained from the IEP zooplankton monitoring program, in which samples have generally been taken monthly in March and...
November and twice monthly (once monthly since 1994) from April to October, 1972 to 1999 (Orsi & Mecum 1986, 1996, Kimmerer & Orsi 1996). Chl a concentration was obtained from 1975 to 1999 from the IEP zooplankton and water quality (Lehman 1992) monitoring programs, which used the same methods and were combined in 1995. Data were analyzed for 2 salinity ranges: 0.5 to 6 psu (LSZ, Kimmerer et al. 1998) and 6 to 20 psu; and 2 seasons: spring (March to May) and summer (June to October). The salinity ranges were based on faunal breaks determined in previous analyses (e.g. Kimmerer et al. 1998). Data were analyzed by salinity range rather than geographic location because planktonic species in brackish regions of estuaries vary most strongly by salinity (Laprise & Dodson 1994, Kimmerer et al. 1998).

Seasons were selected to correspond roughly with larval and juvenile stages of the fishes of interest, and the availability of data from the selected salinity ranges. Analysis of intra-seasonal patterns is described below. The log-transformed data within each salinity range were averaged within months and then within seasons.

Zooplankton data included abundance of the rotifer Synchaeta bicornis, the mysid Neomysis mercedis, and adults of the copepod Eurytemora affinis, all averaged over stations in the LSZ. Rotifers and mysids are uncommon in spring and their abundance was averaged only over summer months. Abundance of the copepod Acartia spp., not identified to species in the monitoring program but comprising at least 3 species (unpubl. data), was analyzed from stations at a salinity of 6 to 20 psu. For chl a and copepod abundance, for which data were available over several months, I performed a principal components analysis (PCA) of annual patterns by month to determine modes of variability. Following Jassby (1999) and Jassby et al. (2002), I constructed a table of means by month (column) and year (row), then treated each column as a separate variable in the PCA. In contrast to chl a in the Delta (Jassby et al. 2002), which had separate spring and summer modes of variability, only a single mode dominated the patterns in the data presented here.

Abundance indices for juvenile life stages of fish and shrimp were obtained from IEP reports based on 3 routine surveys. The fall midwater trawl survey obtained data during 1967 and 2000 (except 1974 and 1979), monthly from September to December at 57 to 113 (median 88) stations in the northern estuary. Ten min oblique tows from near the bottom to the surface were...
taken with a 3.7 m square trawl with a variable mesh body (20.3 to 2.5 cm) and a 1.3 cm stretch mesh cod end. The annual midwater trawl (MWT) abundance index was calculated for each survey as the mean catch per tow over each of 17 regions multiplied by the volume in that region, summed over all regions and then over all months. The San Francisco Bay study (Armor & Herrgesell 1985) took samples monthly all year during 1980 and 2000, except in winter months since 1989, using both an otter trawl and a MWT. Abundance indices were calculated similarly to those from the fall MWT survey using the otter trawl for demersal species and the MWT for other species.

Abundance indices for striped bass *Morone saxatilis* and delta smelt *Hypomesus transpacificus* were obtained from a summer townet survey (Turner & Chadwick 1972). From 1959 to 2000 (except for 1966), 2 to 5 surveys were conducted at approximately 2 wk intervals starting in June. The median number of stations used was 27. The striped bass YOY index was interpolated to the time when the mean size of the young striped bass in the catch was 38 mm. The delta smelt index was calculated from the mean abundance in the 2 surveys used to determine striped bass abundance (Miller 2000).

Abundance of Sacramento splittail was incremented by 1, and that of starry flounder by 10, to account for 0s in log transformation as for zooplankton. Data for starry flounder were abundance at Age-1, related to flow conditions during the previous year, because Age-0 starry flounder are not collected reliably. Otherwise, data were for Age-0 fish and shrimp, related to flow conditions during the same year.

Abundance indices of striped bass and Pacific herring were autocorrelated because of effects of spawning stock size; therefore, indices of early survival were used instead of abundance indices. Abundance of young striped bass has been affected by declining egg production due to a shrinking adult population; hence, a survival index for young striped bass was calculated for 1969 to 1994 (Kimmerer et al. 2001). This index is the log ratio of the summer townet index of young striped bass (Turner & Chadwick 1972) to potential egg production by the adult population. Potential egg production was calculated by multiplying estimates of age-specific fecundity by abundance at age based on Petersen mark-recapture estimates (Stevens et al. 1985, Kimmerer et al. 2000). Corrections were also made for the fraction of each age class that is mature and that actually migrates to the spawning ground (Stevens et al. 1985).

<table>
<thead>
<tr>
<th>Data type</th>
<th>Frequency</th>
<th>Source</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll (chl a)</td>
<td>Monthly 1975 to</td>
<td>Water quality and zooplankton monitoring</td>
<td>Whole chl a averaged over all stations in the low salinity zone (LSZ)</td>
</tr>
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<td></td>
<td>1999</td>
<td>programs</td>
<td>(salinity 0.5 to 6) and in salinity 6 to 20, separately for spring (March to May) and summer (June to October).</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>1 to 2 mo⁻¹ March</td>
<td>Zooplankton monitoring programs (Orsi &amp; Mecum 1986)</td>
<td>Three zooplankton taxa in the LSZ: rotifers (<em>Synchaeta bicornis</em>) and mysids (<em>Neomysis mercedis</em>) in summer and copepods (<em>Eurytemora affinis</em>) separately in spring and summer. Also <em>Acartia</em> spp. in spring and summer in 6 to 20 psu.</td>
</tr>
<tr>
<td>Midwater trawl (MWT) indices</td>
<td>Annual 1967 to 2000</td>
<td>Fall MWT survey</td>
<td>Indices of abundance and salinity data for longfin smelt, American shad, Sacramento splittail.</td>
</tr>
<tr>
<td>Annual abundance indices</td>
<td>Annual 1980 to 2000</td>
<td>San Francisco Bay Study (Armor &amp; Herrgesell 1985)</td>
<td>Indices of abundance for bay shrimp, Pacific herring, starry flounder; salinity data for fish and shrimp</td>
</tr>
<tr>
<td>Striped bass and delta smelt Index</td>
<td>Annual 1959 to 2000</td>
<td>Summer tow net survey (Turner &amp; Chadwick 1972)</td>
<td>Indices of abundance interpolated to mean length of 38 mm for striped bass; abundance in the last 2 surveys for delta smelt.</td>
</tr>
<tr>
<td>Potential striped bass egg production</td>
<td>Annual 1968 to 1994</td>
<td>Adult striped bass survey, fecundity estimates (Stevens et al. 1985)</td>
<td>Total egg production estimate based on abundance estimate × age-specific fecundity × maturity/migration corrections</td>
</tr>
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Table 2. Data sources used in this study
I calculated a survival index for Pacific herring as the ratio of the juvenile index from the Bay study MWT survey to egg abundance. Egg abundance was estimated by the Department of Fish and Game separately for eggs attached to vegetation, intertidal hard substrate and pier pilings, then combined into a single annual estimate (Watters & Oda 2001, based on Spratt 1981).

The hypotheses tested for each taxon were: (1) the response variable is related to $X_2$; and (2) the response variable changed between 1987 and 1988. The latter change would be consistent with an effect of the clam Potamocorbula amurensis if its filtration rate underwent a step change from 0 before to a high value after that time. This seems to have been the case: clam abundance in Suisun Bay went from 0 to over 2000 m$^{-2}$ in 1 mo (Alpine & Cloern 1992) and has since exceeded 1400 m$^{-2}$ in $\frac{1}{2}$ of the samples taken in Suisun and San Pablo Bay year-round (IEP data). Routine benthic monitoring includes too few stations for an estimate of interannual variability of clam abundance adequate for detailed testing of effects of clams on the pelagic food web. In addition, it does not report size of clams, which is needed to estimate filtration rate. Estimates of community filtration rates in Suisun Bay suggest that Potamocorbula amurensis is probably responsible for the continued low chl a concentrations there (J. Thompson, US Geological Survey, pers. comm.).

The fundamental statistical model fitted to the abundance data was a regression on $X_2$ with a dummy variable YearCat, which was 0 for years up to 1987 and 1 thereafter. The model was then:

$$Y_i = \alpha X_{2i} + \beta \text{YearCat}_i + \gamma X_{2i} \times \text{YearCat}_i + \epsilon_i \quad (1)$$

where $Y$ is the log-transformed abundance or survival index or value, $\alpha$, $\beta$ and $\gamma$ are parameters to be estimated, $\epsilon_i$ is the error term, and subscript $i$ refers to year. This model was refined as necessary. Where the interaction term was significantly different from 0, the data set was broken into 2 parts corresponding to YearCat for separate estimates of $\alpha$. When $\gamma$ was not different from 0, and in all cases to estimate $\beta$, the model was fitted without the interaction term.

To illustrate the range of habitat used by the species considered here, salinity ranges were determined for each species of fish and shrimp from the San Francisco Bay study, which has the best coverage of the salinity range of the sampling programs. Mean abundance was calculated for each of 25 salinity ranges or ‘bins’ containing approximately equal numbers of samples. Data from the zooplankton survey were treated similarly, except the salinity bins had linearly decreasing numbers of samples with increasing salinity to account for the heavy weighting of sampling toward freshwater. Minimum bin size was 25 samples in that case. Mean salinity and mean abundance by bin were calculated, and the 25th, 50th and 75th percentiles of relative abundance in salinity space were interpolated.

Trawl sampling is inefficient, and its efficiency can vary with turbidity (Rozas & Minello 1997), which increases in the estuary under high flow conditions (Buchanan et al. 1995, Buchanan & Schoellhamer 1996). Assessing this potential source of bias directly is difficult because turbidity also covaries with season, salinity, and particularly wind and tidal currents. To determine whether such bias was likely, I analyzed mean length of common fish species and proportion of adults in the shrimp catch, assuming that bias due to turbidity would be reflected both in lower catches and a smaller proportion of large individuals in samples from clearer water. Using only samples from which at least 20 individuals had been measured for each species, with data aggregated over seasons of high abundance and similar size distributions, I then determined regressions of mean length versus secchi depth as a measure of turbidity.

Data analyses relied on an exploratory approach with an emphasis on graphical techniques (Cleveland 1973). Assumptions of normality, homoscedasticity, lack of autocorrelation in residuals and lack of excessive influence of single points were tested by examining standard plots of residuals including autocorrelation functions. Cases in which some points had high influence were examined further using robust techniques (Venables & Ripley 1997); the few cases where the results were qualitatively different from the unweighted linear model are discussed below. In the initial analysis of delta smelt abundance, there was evidence that the fitted model was inappropriate, as determined by plots of residuals. Further analysis was done with this species to determine a more suitable model using tree regression to determine the timing of change in abundance. However, for comparability most of the discussion addresses the model described above.

RESULTS

Salinity ranges of most species were broad (Fig. 2). The median salinity values ranged from 0.3 for American shad to 19 for Pacific herring. All but 3 of these species had median salinity between 0.5 and 6, i.e. their distributions overlapped substantially with the LSZ, but large parts of these populations are outside of the LSZ. Trophic interactions are likely among some of these species by virtue of their spatial and temporal overlap as well as feeding modes (e.g. Fig. 3 in Jassby et al. 1995).
The time course of freshwater flow into the estuary and $X_2$ indicates several high flow periods and several droughts (Fig. 3). The highest, i.e. most landward, $X_2$ values occurred during a severe drought in 1976 to 1977, and an extended drought lasting from 1984 through 1992 except for March 1986.

Chl $a$ concentration and copepod abundance showed single modes of variability based on the seasonal PCA (Table 3). The first PC and the mean annual values for each month were correlated with a coefficient of at least 0.64 (up to 0.99). The first PC showed a strong decline around 1987 and was unrelated to $X_2$ (coefficients $\alpha$ and $\gamma$ in Eq. [1] not significant, $p > 0.1$).

Time courses of the response variables show rather consistent declines in the late 1980s among the lower trophic levels, particularly in summer (Fig. 4). Although the specific temporal pattern varied among responses, chl $a$ and abundance of 4 zooplankton taxa were lower after 1987 than before. This contrasts with the overall pattern among fish and shrimp (Fig. 5).

Few of these showed a pattern of annual abundance or survival index that was consistently lower after 1987 than before, although delta smelt abundance was lower after 1981 than before (Fig. 5E).

A clear contrast also exists between the taxa in lower trophic levels, and the fish and shrimp in their relationships to $X_2$ (Figs. 6, 7 & 8, Table 4). Taxa in lower trophic levels had generally weak responses to flow. With several exceptions discussed below, fish and shrimp generally had strong relationships to $X_2$ and relatively small changes between the 2 periods. With the exception of delta smelt, the patterns of change of populations of higher and lower trophic levels clustered separately (Fig. 6).

Details of the patterns summarized in Fig. 6 are presented in Table 4 and Figs. 7 & 8. Chl $a$ in the LSZ has never had a strong relationship with $X_2$, although the relationship in the summer data up to 1987 may be unimodal (Fig. 7B), as found by Jassby & Powell (1994). Although the interaction term for spring chl $a$ in the LSZ was statistically significant, the slopes versus $X_2$ were rather small both before and after 1987 (Table 4). The mean chl $a$ value decreased after 1987 by about 3-fold in spring and 4-fold in summer (Figs. 4A,B &
The period up to 1987 was characterized by phytoplankton blooms that typically lasted most of the spring and summer, with long-term geometric mean chl a around 10 g l⁻¹. After 1987, chl a values have been almost uniformly low through spring and summer except for 1 moderate spring bloom in 1998 (Fig. 4A). Chl a at higher salinity had a similar pattern to that in the LSZ, except for the lack of an interaction term in spring (Fig. 6, Table 4).

The abundance of the copepod *Eurytemora affinis* (Figs. 4C,D & 7C,D) declined by about 7-fold in spring and 7-fold in summer after 1987. Springtime abundance had a significant interaction, forcing a split into the 2 time periods, with the post-clam period having a significant negative relationship with X₂ (Table 4). The copepod *Acartia* spp. (Figs. 4E,F & 7E,F) declined by roughly the same amount as *E. affinis*. The X₂ term in spring was not statistically significant, but this result was influenced by 2 low points in 1996 and 1997. This increased the error variance and may have obscured a slope of about -0.02 as determined by robust regression (Venables & Ripley 1997). In summer, there was no effect of flow on *Acartia* abundance.

The rotifer *Synchaeta bicornis* is typically abundant in the LSZ in summer. Abundance was unrelated to X₂ and declined about 11-fold between the 2 time periods (Figs. 4G & 7G). The mysid *Neomysis mercedis* (Figs. 4H & 7H) was previously abundant in the LSZ in summer but declined about 50-fold after 1987. The response of *N. mercedis* to X₂ changed significantly between the 2 periods, with a negative slope through 1987 (higher at high flow) and a steep positive slope thereafter (Table 4).

Abundance patterns of *Eurytemora affinis* and *Neomysis mercedis* provide an incomplete picture because these species were at least partially replaced by other species of somewhat similar life history (Orsi & Ohtsuka 1999). The decline in biomass of calanoid copepods and total mysids was much smaller than those for the single species indicated in Fig. 4. Thus, although there is a clear response of individual species to the step change after 1987, the change in the food environment for higher trophic levels was not so sharp, in spite of the large decline in chl a.

All of the fish and shrimp, except delta smelt, had negative relationships with X₂, indicating higher abundance at high flow, and 2 of them had lower intercepts after 1987. The bay shrimp *Crangon franciscorum* (Figs. 5A & 8A) had a significant relationship with X₂ that had not appeared to change since 1988, although both the lowest and highest residuals around

![Fig. 4. Time course of plankton abundance measures.](image)

![Fig. 5. Time course of fish and shrimp abundance indices or, where noted, survival indices.](image)
the $X_2$ trend line were observed after 1988, indicating a possible transient response either to the change in the food web or to the extended drought from 1985 to 1992.

Starry flounder (Figs. 5B & 8B) had a significant relationship with $X_2$ that declined in intercept by nearly 4-fold. Survival of Pacific herring (Figs. 5C & 8C) had a weak relationship with $X_2$ and no change over time. American shad had a weak but significant relationship to $X_2$; but with a significant effect of time period by which abundance increased after 1987 (Fig. 5D).

The 2 smelt species had strikingly different patterns of abundance and response to $X_2$. Delta smelt abundance index had no discernible relationship to $X_2$ and appeared somewhat lower in abundance in the later time period than before (Figs. 5E & 8E). However, tree regression and examination of plots (Fig. 5E) showed the data series to be most effectively divided between 1981 and 1982 rather than 1987 and 1988. Analysis as in Eq. (1) but with a step change between 1981 and 1982 had a significant interaction; subsequent regressions on the data from the 2 time periods showed a positive relationship with $X_2$ during the period up to 1981 and a negative but non-significant relationship from 1982 and 2000. By contrast, longfin smelt abundance index (Figs. 5F & 8F) had the strongest relationship with $X_2$ and a 4-fold decline after 1987, with no significant change in slope (interaction term $0.018 \pm 0.022$, $p > 0.1$).

Abundance of Sacramento splittail (Figs. 5G & 8G) and survival of striped bass from egg to YOY (Figs. 5H & 8H) varied negatively with $X_2$ and had no discernible change following 1987.

Size distributions of fish and proportion of adult shrimp in catches were analyzed for potential effects of water clarity for several species. Data were obtained from the Bay study for Pacific herring, longfin smelt and bay shrimp in April to July, and striped bass in July to September, and from the fall midwater trawl survey for American shad, longfin smelt and striped bass. In no case was the slope of a linear regression of mean length (or proportion adults in shrimp catch) versus log of secchi depth significantly negative, and several were significantly positive ($p < 0.05$, linear regressions). This suggests that water clarity did not have a substantial effect on catchability by size, and relationship...
ships of abundance to flow were likely not due to

covariation of water clarity with both flow and catcha-

bility of the fish and shrimp.

**DISCUSSION**

The results presented here contrast with findings
from other estuaries. Several mechanisms have been
reported for positive effects of flow on populations
(Drinkwater & Frank 1994), including bottom-up
effects due to nutrient stimulation (Aleem 1972, Sut-
cliffe 1972, 1973, but see Sinclair et al. 1986) or
increased stratification with flow (Skreslet 1997), and
suppression of predators on benthos by low salinity
(Wilber 1992, Livingston et al. 2000). Catch rates of
several fishery species were related to freshwater flow
in an Australian estuary, although much of that rela-
tionship may have been due to vulnerability of the fish
rather than population size (Loneragan & Bunn 1999).
As discussed below, none of these mechanisms is con-
sistent with the data from the San Francisco Estuary. In
addition, negative effects of freshwater flow on estuar-
2000) were nearly absent in estuarine-dependent spe-
cies from the San Francisco Estuary. Abundance of
marine species within the San Francisco Estuary may
respond negatively to flow due simply to seaward dis-
placement of their habitat, and therefore, population
centers; however, this would be a distributional rather
than a population response. Negative effects appar-
etly due to osmotic stress have been observed in the
benthos (Nichols et al. 1990), but pelagic organisms
are able to move with the water and may be relatively
unaffected by salinity fluctuations (Laprise & Dodson
1993).

**Mechanisms for flow effects**

Bias is an unlikely explanation for the flow effects
reported here. The most likely source of bias is increas-
ing catchability with increasing turbidity (Rozas & Minello 1997). However, turbidity depends mainly on
tidal currents and wind, and is affected by freshwater
flow mainly during extreme flow events. For example,
suspended solids concentrations throughout the estu-
ary were not much different between 1994, a drought
year, and 1995, a high-flow year, except during flow
peaks (Buchanan et al. 1995, Buchanan & Schol
hamer 1996). Furthermore, mean length of common
fish species or proportion of adult bay shrimp did not
increase with turbidity as measured by secchi disk.

Although mechanisms behind the abundance flow
relationships in higher trophic levels cannot be de-
duced from correlative analyses, these mechanisms
are unlikely to arise from effects occurring at the base
of the food web. A simplified view of the food web of
the northern San Francisco Estuary (Fig. 9) illustrates
the alternative causal pathways between physical
forcing, particularly freshwater flow and biological re-
sponses. For freshwater flow to influence fish and
shrimp through the food web (Fig. 9, Mechanisms 1 to
3, and 4 for zooplankton) would require first that lower
trophic levels have positive responses to flow, and that
these responses propagate up the food web. Neither of
these mechanisms is supported by the results pre-
sented here. Taxa in lower trophic levels either did not
respond to flow, or they responded inconsistently by
season, or with different slopes up to versus after 1987.
Most taxa at higher trophic levels, which feed mainly
on copepods and mysids during early life, had positive
relationships to flow that did not change in slope after
1987, although several changed in intercept, 2 nega-
tively and 1 positively. The large change noted for
delta smelt (Fig. 8E, Table 4) apparently occurred well
before the step change at the base of the food web
(Fig. 5E). Thus, the flow response at higher trophic
levels was largely uncoupled from variability in lower
trophic levels.

![Fig. 8. Timescale of fish and shrimp abundance or, where
noted, survival indices. Details as for Fig. 4. Regression sta-
tistics in Table 4. Taxa as for Fig. 5](image-url)
Table 4. Summary of parameters of models generalized in Eq. (2) for biological response variables, with estimated 95% confidence limits. Values in **bold** are significantly different from 0 at \( p < 0.05 \) (2-tailed). The basic model was that in Eq. (1) without an interaction unless noted. Where interactions were significant, data were split into 2 groups for regression; however, the magnitude of the step term below and in Fig. 6 was determined without the interaction term for comparability. \( S \) under response variable refers to salinity.

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Response variable</th>
<th>Averaging period</th>
<th>( n )</th>
<th>( \alpha ) in Eq. (1) ( (X_\alpha) )</th>
<th>( \beta ) in Eq. (1) ( (\text{step after 1987}) )</th>
<th>YearCat</th>
<th>Years</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton</td>
<td>Chlorophyll (chl a) ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey Mar to May</td>
<td>24</td>
<td>0.009 ± 0.011</td>
<td>−0.4 ± 0.21</td>
<td>1975–1987</td>
<td>1988–1999</td>
<td>No data for 1995; significant interaction (( \gamma \neq 0 ))</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>Chl a ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey Jun to Oct</td>
<td>25</td>
<td>−0.002 ± 0.010</td>
<td>−0.63 ± 0.17</td>
<td>1975–1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>Chl a ( (S = 6 \text{ to } 20) )</td>
<td>Survey Mar to May</td>
<td>24</td>
<td>−0.004 ± 0.010</td>
<td>−0.48 ± 0.22</td>
<td>1975–1999</td>
<td></td>
<td>No data for 1995</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>Chl a ( (S = 6 \text{ to } 20) )</td>
<td>Survey Jun to Oct</td>
<td>25</td>
<td>−0.004 ± 0.009</td>
<td>−0.59 ± 0.15</td>
<td>1975–1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eurytemora affinis</em></td>
<td>Abundance + 10 ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey Mar to May</td>
<td>16</td>
<td>−0.004 ± 0.019</td>
<td>−0.86 ± 0.32</td>
<td>1972–1987</td>
<td>1988–1999</td>
<td>Significant interaction (( \gamma \neq 0 ))</td>
</tr>
<tr>
<td><em>Eurytemora affinis</em></td>
<td>Abundance + 10 ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey Jun to Oct</td>
<td>28</td>
<td>0.001 ± 0.01</td>
<td>−1.88 ± 0.20</td>
<td>1972–1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acartia spp.</em></td>
<td>Abundance + 10 ( (S = 6 \text{ to } 20) )</td>
<td>Survey Mar to May</td>
<td>25</td>
<td>−0.015 ± 0.02</td>
<td>−0.83 ± 0.44</td>
<td>1972–1999</td>
<td>1974, 1975, 1995 missing</td>
<td></td>
</tr>
<tr>
<td><em>Acartia spp.</em></td>
<td>Abundance + 10 ( (S = 6 \text{ to } 20) )</td>
<td>Survey Jun to Oct</td>
<td>28</td>
<td>−0.005 ± 0.02</td>
<td>−1.64 ± 0.38</td>
<td>1972–1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Synchaeta bicornis</em></td>
<td>Abundance ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey Jun to Oct</td>
<td>28</td>
<td>0.006 ± 0.019</td>
<td>−1.03 ± 0.33</td>
<td>1972–1999</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Neomysis mercedis</em></td>
<td>Abundance ( (S = 0.5 \text{ to } 6) )</td>
<td>Survey May to Oct</td>
<td>15</td>
<td>−0.036 ± 0.021</td>
<td>−1.67 ± 0.39</td>
<td>1973–1987</td>
<td>1988–1999</td>
<td>Significant interaction (( \gamma \neq 0 ))</td>
</tr>
<tr>
<td>Bay shrimp</td>
<td>Abundance index Mar to May</td>
<td>21</td>
<td>−0.024 ± 0.011</td>
<td>−0.04 ± 0.26</td>
<td>1980–2000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Starry flounder</td>
<td>Abundance index + 1 Mar to Jun</td>
<td>21</td>
<td>−0.023 ± 0.015</td>
<td>−0.58 ± 0.36</td>
<td>1980–2000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific herring</td>
<td>Survival index Jan to Apr</td>
<td>20</td>
<td>−0.021 ± 0.022</td>
<td>−0.01 ± 0.5</td>
<td>1980–2000</td>
<td>No data for 1994</td>
<td></td>
<td></td>
</tr>
<tr>
<td>American shad</td>
<td>Abundance index Feb to May</td>
<td>32</td>
<td>−0.014 ± 0.009</td>
<td>0.25 ± 0.22</td>
<td>1967–2000</td>
<td>No data for 1974, 1979</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delta smelt</td>
<td>Summer abundance index Feb to Jun</td>
<td>39</td>
<td>0.017 ± 0.022</td>
<td>−0.44 ± 0.33</td>
<td>1959–1987</td>
<td>Significant interaction; but see text. No data for 1966–1968</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longfin smelt</td>
<td>Abundance index Jan to Jun</td>
<td>32</td>
<td>−0.053 ± 0.012</td>
<td>−0.60 ± 0.27</td>
<td>1967–2000</td>
<td>No data for 1974, 1979</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sacramento splittail</td>
<td>Abundance index Feb to May</td>
<td>31</td>
<td>−0.031 ± 0.013</td>
<td>−0.07 ± 0.3</td>
<td>1967–2000</td>
<td>No data for 1974, 1979</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Striped bass</td>
<td>Survival index Apr to Jun</td>
<td>25</td>
<td>−0.027 ± 0.012</td>
<td>−0.08 ± 0.3</td>
<td>1969–1994</td>
<td>No data for 1983</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Additional information also fails to support Mechanisms 1 to 3 (Fig. 9). According to the agricultural model (Nixon et al. 1986), increasing nutrient or organic inputs with increasing flow results in stimulation that propagates to higher trophic levels (Fig. 9, Mechanisms 1 and 2). That model would require a causal chain by which increased nutrient input with high flow resulted in higher phytoplankton production and biomass, with increases subsequently passed up through the food web. However, phytoplankton production in the San Francisco Estuary is most commonly limited by light rather than nutrients (Arthur & Ball 1979, Cole & Cloern 1984, Cloern 1999), and nutrient concentrations in the northern estuary are generally high (Hager & Schemel 1992).

Phytoplankton blooms can also occur through stratification, which may increase with freshwater flow (Fig. 9, Mechanism 3; Cloern 1991, Skreslet 1997). However, in the San Francisco Estuary, such blooms appear to be ephemeral (Cloern 1991). The PCA results suggested the principal mode of variability of chl a and copepod abundance in all months was the step after 1987. Furthermore, chl a concentration showed little response to freshwater flow either before or after Potamocorbula amurensis became abundant (Fig. 7A,B). In the Delta, in spring, chl a actually decreased with increasing flow, apparently because of decreasing residence time (Jassby et al. 2002). Thus, there is no evidence that seasonally averaged phytoplankton biomass responded to flow through either increased nutrient loading or increased stratification with flow.

Exogenous organic carbon may provide important energy supplies to estuaries (e.g. Smith & Hollibaugh 1993, Kemp et al. 1997). The supply rate of organic carbon to a brackish estuary increases with increasing freshwater flow, mainly because of river-borne inputs (Jassby et al. 1993, 1995). Most of the bioavailable carbon in the San Francisco Estuary arises from phytoplankton (Jassby et al. 1993, Canuel et al. 1995, Jassby & Cloern 2000). Although biomass in the Delta decreased with increasing flow in spring, loading still increased (Jassby et al. 1993, 2002 Fig. 8A). With an increase in the supply rate of bioavailable carbon with flow, bacterial production could increase with flow (Fig. 9, Mechanism 2). There is no information on the response of bacterial production to flow, although bacterial abundance may have declined following the spread of Potamocorbula amurensis, which is capable of filtering bacteria from the water column (Werner & Hollibaugh 1993, Hollibaugh & Wong 1996). In any case, for the stimulation of bacterial production due to increased carbon loading to reach higher trophic levels would require equivalent levels of response to flow in the intermediate trophic steps, i.e. zooplankton and particularly rotifers (Holst et al. 1998); however, this was not observed.

It is unlikely that the lower trophic levels responded to flow in production but not in biomass. Jassby et al. (2002) argued that primary production in the Delta followed trends in chl a concentration, and the same argument holds for Suisun and San Pablo Bays. Reproductive rate of the copepod Eurytemora affinis did not vary with flow or chl a, nor did it change after the arrival of Potamocorbula amurensis (Kimmerer et al. 1994). Similarly, no changes were detected in fecundity of Neomysis mercedis (Orsi & Mecum 1996). Data are unavailable to estimate production of other planktonic taxa, but without an increase in food supply with flow, there is no reason to expect specific growth rate to increase with increasing flow for any of these taxa.

The contrast between results for the lower and higher trophic levels (Fig. 6, see below) suggests that different mechanisms influence abundance patterns of these groups. There is evidence of bottom-up effects in the pelagic food web propagating from the decline in phytoplankton through rotifers, copepods and mysids,
and into starry flounder and longfin smelt, but apparently leaving other fish and shrimp unaffected. However, these bottom-up effects appear unrelated to the X₂ relationships of fish and shrimp. This implies that mechanisms underlying responses of fish and shrimp may occur more directly, such as through changes in physical habitat (Fig. 9). To assess these effects will require further research, since the statistical analyses reported here are insufficient to establish causes.

Bennett & Moyle (1996) described several alternative mechanisms by which flow could influence young stages of fish. For few species are data available to support or reject these mechanisms, although the list of possible mechanisms for any 1 species can be narrowed. The mechanisms underlying flow effects probably operate in the region or range of salinity where each species is found during early life (Fig. 2). For example, floodplain inundation may favor splittail recruitment through improved access to shallow foraging, spawning or rearing habitat (Fig. 9, Mechanism 5; Sommer et al. 1997). This mechanism could also affect American shad and some other species in freshwater, but is unlikely to affect those found mainly in brackish to saline water. Species such as bay shrimp, starry flounder and herring could be affected by changes in gravitational circulation in the seaward reaches of the estuary, since these species hatch in or near the ocean, and presumably use net landward bottom currents to move into and up the estuary. This mode of recruitment is common in decapod crustaceans and flatfish (e.g. Cronin & Forward 1979, Harden Jones et al. 1979, Forbes & Benfield 1986, Christy & Morgan 1998).

The main point, though, is that the mechanisms underlying flow effects on each of the species are apparently different. This implies in turn that these mechanisms are unlikely to be general, but rather that they arise through specific features of the San Francisco Estuary that may not exist in other estuaries. If they arise through specific features of the San Francisco Estuary that may not exist in other estuaries, they may not operate in the region or range of salinity where each species is found during early life (Fig. 2).

The lack of response of certain fish and shrimp species to this change is somewhat surprising. The planktonic species comprise much of the food supply for larvae, juveniles and smaller adults of striped bass and other fish, and epibenthic shrimp in the estuary (Heubach et al. 1963, Sitts & Knight 1979, Meng & Orsi 1991, Bennett & Moyle 1996, Nobriga 1998). For example, delta smelt larvae feed mostly on Eurytemora affinis, yet the mechanism underlying flow effects on these species is not clear. The principal basis for these effects was an increase in water clarity during a prolonged drought, apparently causing an increase in primary production (Livingston et al. 1997). Thus, the mechanisms for effects of flow, and the overall responses of the food webs, appear to differ between Apalachicola Bay and the San Francisco Estuary. The common lesson to be learned from these 2 estuaries appears to be the complexity of the food webs (Livingston et al. 1997), whose response to rather dramatic forcing is difficult to interpret or generalize.

Response of the food web to perturbation

The introduction of Potamocorbula amurensis was accompanied by a number of rapid changes at the base of the food web. The decline in chl a concentration, which extended far into the Sacramento-San Joaquin delta (Jassby et al. 2002), suggests a substantial, system-wide loss of organic input. Although riverine sources of organic carbon are large, the supply of labile carbon to the estuary is dominated by phytoplankton (Jassby et al. 1993, 2002, Jassby & Cloern 2000). Even before this decline, primary production in the San Francisco Estuary was at the low end of the range for estuaries (Boynton et al. 1982). Furthermore, evidence is growing that consumer organisms in the San Francisco Estuary are frequently and persistently food-limited (Foe & Knight 1985, Orsi & Mecum 1996, Mueller-Solger et al. 2002, author’s unpubl. data).

Alternative consumers have partially replaced those existing before this event: for example, introduced copepods such as Pseudodiaptomus forbesi have taken the place of Eurytemora affinis (Kimmerer & Orsi 1996), and introduced mysids have partially compensated for the loss of Neomysis mercedis (Modlin & Orsi 1997). Potamocorbula amurensis itself is an additional source of food for a few species listed in Table 1, although it may have suppressed other benthic species (Nichols et al. 1990). Nevertheless, the general trend throughout the northern estuary has been toward decreased organic matter production and plankton abundance with time, particularly following the spread of P. amurensis.

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occurs later in life when they start to consume mysids or small fish (Kimmerer et al. 2000).

Detailed comparisons of diets of fish and shrimp between the 2 time periods have not been made. Nevertheless, differences among the fish and shrimp in response to the downward shift in primary production do not appear to be related to dietary habits, or seasonal or spatial patterns. For example, bay shrimp and starry flounder both feed on benthic and epibenthic prey (Table 1), and both recruit from the ocean in spring, yet starry flounder declined and bay shrimp did not (Fig. 8A,B). The smelt species, American shad, and young striped bass all move down the estuary to brackish water as they develop, and all feed on plankton in open waters (Table 1), but only longfin smelt appeared to respond to the downward shift in production.

Thus, despite the apparently tight coupling between benthic grazing and pelagic production, trophic coupling within the pelagic food web of the San Francisco Estuary may be weak. Complex aquatic food webs in general may be weakly coupled (Strong 1992, Polis & Strong 1996, Micheli 1999) and weak trophic interactions may stabilize food webs (McCann et al. 1998). Aquatic food webs may be uncoupled because of species-specific responses by zooplankton (Runge 1988, McQueen et al. 1989, Pace et al. 1998) or fish (Stein et al. 1995). Direct predatory effects of fish may also act simultaneously with nutrient effects to complicate trophic interactions even in relatively simple food webs (Persson 1997, Vanni & Layne 1997). Furthermore, low efficiency of trophic transfer may allow for weak or nonlinear responses of higher trophic levels to changes at the base of the food web, particularly when changes in phytoplankton are qualitative as well as quantitative (Cushing 1971, Turner 2001). On the other hand, trophic transfer in some estuaries may peak when larvae of common fish species are present (Mallin & Paerl 1994).

To some extent weak trophic linkages observed in the pelagic food web of the San Francisco Estuary can also be attributed to the open boundaries of the estuary, through which both fish and their food supplies can move, and to extreme temporal variability. In spite of the evidence for strong biological effects at lower trophic levels (e.g. Alpine & Cloern 1992, Kimmerer et al. 1994), the wider distribution, ontogenetic movement and variable seasonal patterns of most fish species may help to spread the risk (Bennett & Moyle 1996), and allow them to take advantage of feeding opportunities not represented by a simple model of the estuarine food web. Because estuarine ecosystems are open, models of estuarine populations and food webs may require a certain degree of exogenous forcing to dampen the effects occurring within the food web.

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LITERATURE CITED


Alpine AE, Cloern JE (1992) Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnol Oceanogr 37:946–955


Laprise R, Dodson JJ (1994) Environmental variability as a factor controlling spatial patterns in distribution and spe-
Sitts RM, Knight AW (1979) Predation by the estuarine shrimps *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun. Biol Bull 156:356–368


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