

Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA

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Abstract: We examined a 36-year record of concurrent midwater trawl and water quality sampling conducted during fall to evaluate habitat trends for three declining fish species in the San Francisco Estuary, California, USA: delta smelt (*Hypomesus transpacificus*), striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*). Generalized additive modeling revealed that Secchi depth and specific conductance were important predictors of occurrence for delta smelt and striped bass, while specific conductance and water temperature were important for threadfin shad. Habitat suitability derived from model predictions exhibited significant long-term declines for each species; the south-eastern and western regions of the estuary exhibited the most dramatic changes. Declines in habitat suitability were associated with anthropogenic modifications to the ecosystem. For delta smelt, an imperiled annual species endemic to the estuary, the combined effects of fall stock abundance and water quality predicted recruit abundance during recent years of chronically low food supply. Our results are consistent with existing evidence of a long-term decline in carrying capacity for delta smelt and striped bass and demonstrate the utility of long-term data sets for evaluating relationships between fish and their habitat.

Résumé : Nous avons examiné des données concomitantes d'échantillonnage au chalut en pleine eau et d'échantillonnage de la qualité de l'eau faites à chaque automne pendant 36 années dans l'estuaire de San Francisco, Californie, É.-U., afin d'évaluer les tendances de l'habitat chez trois espèces de poissons en déclin, soit l'éperlan du delta (*Hypomesus transpacificus*), le bar rayé (*Morone saxatilis*) et l'alose fil (*Dorosoma petenense*). Un modèle additif généralisé montre que la profondeur de Secchi et la conductance spécifique sont d'importantes variables explicatives de la présence de l'éperlan du delta et du bar rayé, alors que la conductance spécifique et la température de l'eau le sont pour l'alose fil. Les prédictions du modèle indiquent une diminution significative à long terme de la qualité de l'habitat pour chaque espèce; les régions du sud-est et de l'ouest de l'estuaire montrent les changements les plus spectaculaires. Le déclin de la qualité de l'habitat est associé à des modifications anthropiques de l'écosystème. Chez l'éperlan du delta, une espèce annuelle, menacée et endémique à l'estuaire, les effets combinés de l'abondance des stocks à l'automne et de la qualité de l'eau expliquent l'abondance du recrutement durant les années récentes de sources de nourriture chroniquement limitées. Nos résultats confirment les indications existantes d'un déclin à long terme du stock limite de l'éperlan du delta et du bar rayé; ils démontrent l'utilité des banques de données couvrant de grandes périodes pour l'évaluation des relations entre les poissons et leur habitat.

[Traduit par la Rédaction]

Introduction

There have been worldwide declines in production and yield of many estuarine-dependent fishes resulting from overfishing, pollution, and habitat alterations (Houde and Rutherford 1993). These trends have coincided with substantial long-term changes in fish species composition and abundance in developed North American estuaries (Matern et al. 2002; Hurst et al. 2004). Declining yields and changing fish communities suggest that current understanding of fish population dynamics is insufficient to ensure proper management.

The processes underlying fish population dynamics are complex because multiple interacting factors contribute to interannual variation in recruitment and abundance. A fundamental component in the study of population dynamics is the interaction between fish and their habitat. In the broadest sense, habitat can be characterized as the abiotic and biotic factors that are required to support healthy fish populations (Hayes et al. 1996). The abiotic components of habitat often strongly influence the biotic components, particularly in estuaries where freshwater inputs and associated salinity effects are important community-structuring mechanisms (e.g., Bulger et al. 1993; Jassby et al. 1995). Quantifying

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fish–habitat relationships and long-term trends in habitat suitability is critical because abiotic habitat components can affect the population dynamics of fishes in most habitat types (e.g., Cardinale and Arrhenius 2000; Claramunt and Wahl 2000; Rose 2000). Here, we use the term environmental quality (EQ; Rose 2000) to describe abiotic habitat variables that may affect fish population dynamics.

Long-term data sets are essential for the development and evaluation of fish–EQ relationships and time trends (Bray 1996; Rose 2000). Long-term data sets that include a wide range of environmental conditions are particularly useful because they allow researchers to more effectively model the linkages between EQ and fish occurrence (Rose 2000). Moreover, analyses of long-term data sets are needed to understand the effects of management actions. If rehabilitation is desired, then management actions aimed at improving EQ to a pre-existing state can often be determined from existing data. One limitation of empirical data, however, is that it frequently focuses on a particular life stage or time period when sampling was conducted. Thus, it is important to understand the temporal relevance of the sample collections in subsequent model development (Levin and Stunz 2005).

In this study, we quantified fish–EQ relationships in San Francisco Estuary (Fig. 1) using a long-term record (1967–2004) of fish and water quality data concurrently collected during fall (September–December). Our objectives were to (1) develop models relating fish occurrence to EQ, (2) examine temporal and spatial trends in EQ, and (3) determine whether the water quality variables that define EQ can also be linked to fish abundance. Understanding fish–EQ linkages is a principal goal in fisheries science and is of great practical interest in San Francisco Estuary. The estuary is well known for anthropogenic modifications that have highly altered most natural elements of the system, and there have been long-standing concerns about the effect of these modifications on fish populations (Nichols et al. 1986; Bennett and Moyle 1996). Indeed, many fish species have exhibited declines in abundance since long-term monitoring began in the 1950s (e.g., Stevens et al. 1985; Moyle et al. 1992). In recent years, there has also been an apparent step-decline in the abundance of three pelagic species — delta smelt (*Hypomesus transpacificus*), striped bass (*Morone saxatilis*), and threadfin shad (*Dorosoma petenense*) (Fig. 2). These species are the focus of our study. Concern is perhaps greatest for delta smelt, a rare and delicate endemic species listed as threatened under both the California and US Endangered Species Acts; a petition is currently being considered to downgrade delta smelt status to endangered. Water management actions in the estuary are closely tied to protecting delta smelt, even on a daily basis during some portions of the year. Management actions in the estuary receive great attention throughout the state because water diversions from the estuary supply drinking water to over 22 million people in California, in addition to supporting a multibillion dollar agricultural industry. Striped bass and threadfin shad are both introduced species; because they comprise a substantial portion of fish biomass in the ecosystem and support valuable recreational fisheries, their declines are also cause for concern.

Materials and methods

Study area

San Francisco Bay (Fig. 1) forms the largest estuary on the Pacific coast of the United States. The estuary is a drowned river valley separated into different basins by complex bathymetry. Water enters the estuary primarily from California's two largest rivers — Sacramento (from the north) and San Joaquin (from the south) — which drain a 100 000 km² watershed encompassing 40% of California's surface area. The rivers converge in the upper estuary to form the Sacramento – San Joaquin Delta, a 3000 km² network of tidal freshwater channels. From the delta, water flows west into Suisun Bay, through the Carquinez Strait, and enters San Pablo Bay before reaching San Francisco Bay and ultimately the Pacific Ocean. Owing to the Mediterranean climate, freshwater flow entering the estuary varies seasonally, occurring mainly in late winter through spring. The estuary is also subject to extreme interannual variation in freshwater flows, with periodic droughts and floods.

Anthropogenic modifications in this highly altered estuary include the loss of wetlands via draining and diking for agriculture, channel modifications for flood control and navigation, and a variety of water reclamation activities, including storage, conveyance, and large-scale water diversion from the southern delta (Nichols et al. 1986). Major dams located on the Sacramento and San Joaquin rivers, including most of their major tributaries, control flows entering the estuary. One result of these modifications is that water movement through the estuary is highly managed. Through the many large upstream dams; smaller, within-estuary flow control structures; and large water diversion operations in the southern delta, managers have an unparalleled ability to control water movement in the system. One of the ways in which flows are managed in this estuary is to benefit fishes and other organisms by manipulating the position of the estuarine salinity gradient.

Similar to most estuaries, many of the ecosystem components and functions of the San Francisco Estuary exhibit measurable responses to flow (Stevens and Miller 1983; Jassby et al. 1995; Kimmerer 2002). In particular, the abundance or survival of many fishes and invertebrates exhibits a strong relationship with flow entering the estuary, as indexed by the position of the 2‰ isohaline (Jassby et al. 1995; Kimmerer 2002). This index, termed X_2 , is defined as the distance (km) from the Golden Gate Bridge to the location in the estuary where mean bottom salinity is 2‰ (Jassby et al. 1995; Kimmerer 2002). The position of X_2 is seasonally variable based primarily on river flow variation. However, its position can be manipulated and is closely managed to be located in certain regions during specific times of the year to benefit aquatic species.

Data sources and analytical methods

We analyzed long-term data collected from a fall mid-water trawl survey (FMWT) conducted by the California Department of Fish and Game (Stevens and Miller 1983). The survey has been conducted each year since 1967, except that no sampling was done in 1974 and 1979. The FMWT collects a sample (10- to 12-minute tow) at 100 sites four

Fig. 1. Map of the San Francisco Estuary (California, USA) showing fall midwater trawl survey sampling stations. The location of the State Water Project (SWP) and Central Valley Project (CVP) export pumping facilities are also shown.

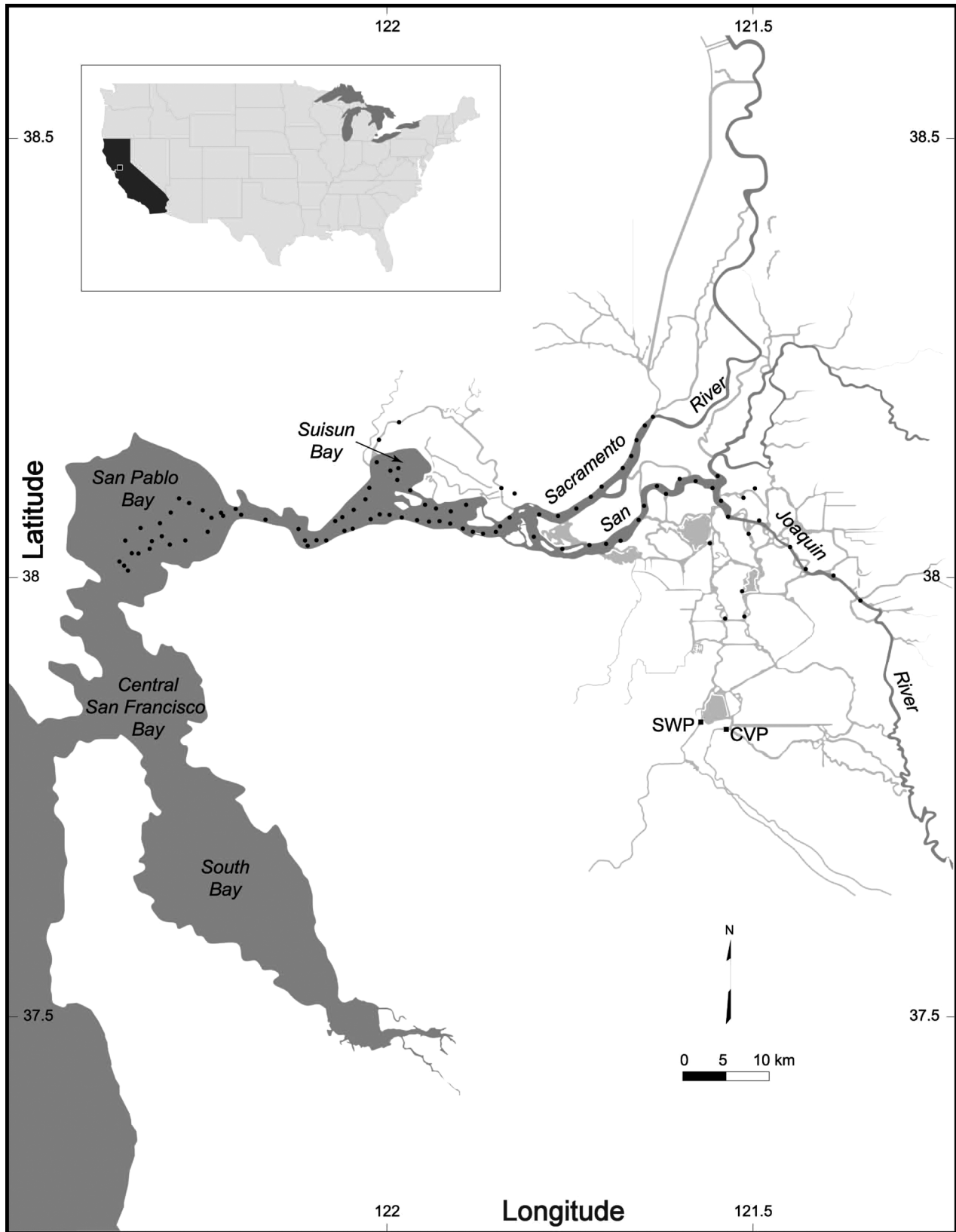
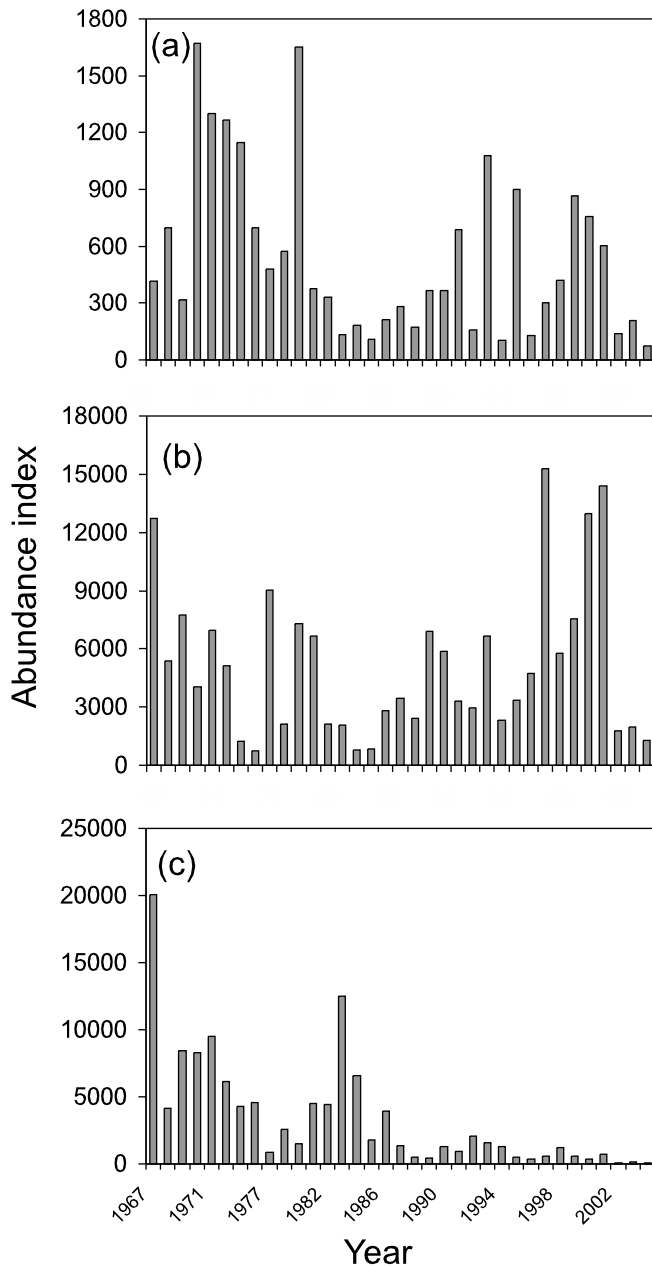


Fig. 2. Time series of abundance indices for (a) delta smelt (*Hypomesus transpacificus*), (b) threadfin shad (*Dorosoma petenense*), and (c) striped bass (*Morone saxatilis*) for the fall midwater trawl survey.



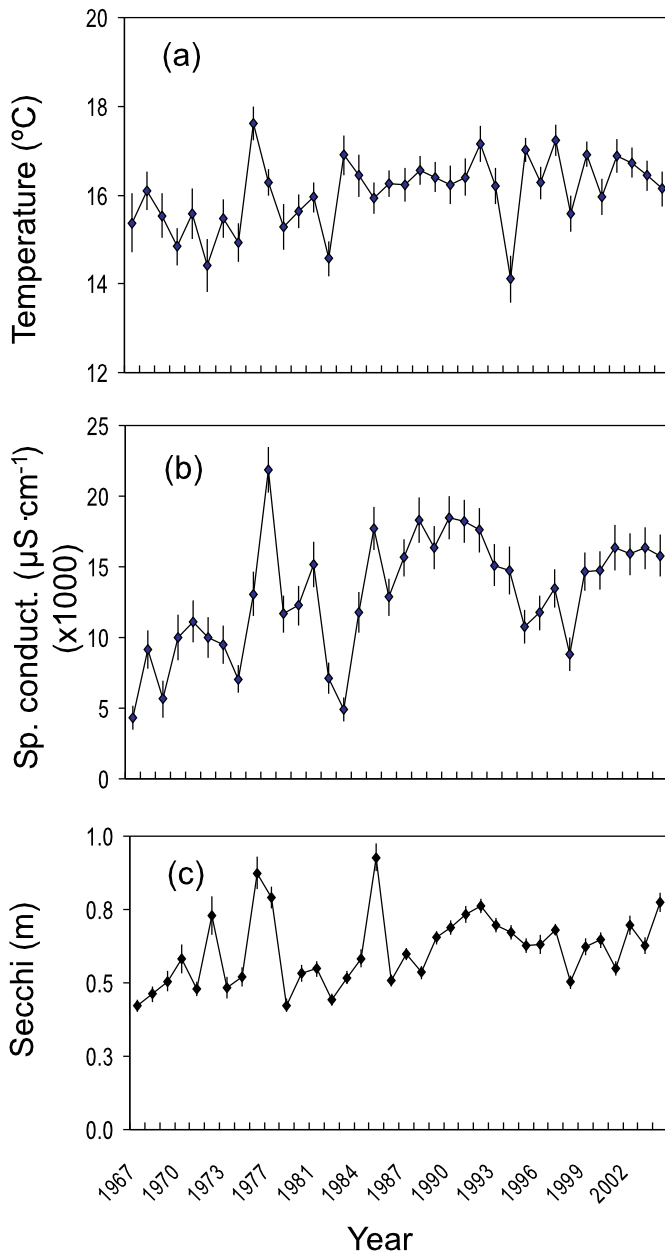
times per year — each month from September to December throughout the freshwater to mesohaline portions of the upper estuary (Fig. 1). The FMWT was originally designed to index the abundance of age-0 striped bass, which is reflected in the dimensions of the net: 17.6 m long with a mouth opening of 3.7 m² and nine tapered panels of stretch mesh from 14.7 to 1.3 cm in the cod end (Stevens and Miller 1983). The FMWT data have been used extensively in analyses of striped bass and delta smelt population dynamics (Turner and Chadwick 1972; Stevens et al. 1985; Moyle et al. 1992). Our analysis focused on age-0 striped bass, delta smelt, and threadfin shad, for which the FMWT is most effi-

cient at capturing. The FMWT stations encompass the distribution of these species and life stages in the estuary. Delta smelt have been observed at 85% of the stations, while striped bass and threadfin shad have been observed at every station. Similar to many river-dominated estuaries, inflow to the system varies substantially from year to year. Thus, while the position of the sampling sites remains consistent, water quality varies interannually, which shifts the center of distribution of the fishes (Dege and Brown 2004). Three water quality variables — temperature (°C), Secchi depth (m), and specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$) — were measured concurrent with each tow, providing a 36-year time series (12 109 samples) of fish and environmental data (Fig. 3).

The FMWT data set provided a uniquely long time series to quantify fish occurrences in relation to water quality. For study objective 1, we used generalized additive models (GAMs) to describe these relationships (Norcross et al. 1997; Stoner et al. 2001). GAMs are semiparametric extensions of generalized linear models that are effective for describing nonlinear relationships between predictor and response variables (Guisan et al. 2002). GAM techniques are data-driven; they do not presuppose a particular relationship between predictor(s) and response variables. Rather, they employ smoothers to characterize the empirical relationships between predictor and response variables (Guisan et al. 2002). Link functions are used to establish relationships between the response variable and a smoothed function of the predictor variables; we used the cubic spline as our smoothing technique in the S-Plus language (Venables and Ripley 1997). Similar to previous studies (Maravelias 1999; Stoner et al. 2001), we used a binomial GAM with logit link function to relate fish occurrence to log-transformed environmental variables. A binary response (fish presence or absence, i.e., occurrence) was used instead of fish abundance to minimize the influence of outliers (i.e., extremely anomalous abundance values) and bias associated with previously reported abundance declines through time. We assumed that habitat preference was constant and that fish would continue to be present under preferred habitat quality conditions, albeit possibly in increasingly lower numbers. We modeled each species separately. Based on our knowledge of the range of each species and laboratory physiology studies (Swanson et al. 2000), we expected that each species would exhibit a unimodal occurrence probability to salinity and temperature and a declining occurrence probability to increasing Secchi depth. We assessed the statistical significance of the GAM results with a χ^2 approximation that tests the ability of each explanatory variable to reduce the deviance in the model (Venables and Ripley 1997).

The GAM analyses generated predicted occurrence probabilities for each species in each sample. We used these capture probabilities as an indicator of habitat suitability through time, which we defined as EQ (study objective 2). We visually evaluated long-term spatial variation in annual trends throughout the estuary using maps created with ArcMap geographic information system (GIS) software (ESRI, Redlands, California). Employing ordinary least squares, we linearly regressed the EQ data for the three fish species at each of the 100 stations against year and used the magnitudes of the slopes to examine long-term EQ trends among sampling stations and across regions of the estuary.

Fig. 3. Time series of (a) water temperature, (b) specific conductance, and (c) Secchi depth for the fall midwater trawl survey. The average and variation based on two standard errors are shown for each variable.



This approach generated 300 separate linear regressions. We incorporated the regression results into GIS maps by scaling GIS polygons representing surface area estimates for each sampling station (R. Baxter, California Department of Fish and Game, 4001 North Wilson Way, Stockton, California, unpublished data) by the corresponding regression slope. This procedure allowed us to create a continuous grid of the water surface area of the estuary with individual cells (polygons) scaled (by color shading) according to the slope coefficients for each species.

Lastly, we tested the ability of the water quality variables that composed EQ to predict delta smelt abundance (study

objective 3). We limited this analysis to delta smelt because it is an annual species. The longevity of striped bass and threadfin shad makes modeling the effects of abiotic factors on abundance markedly more complex and beyond the scope of this paper (e.g., Kimmerer et al. 2001). Further, recent stock–recruit modeling supports the possibility of density dependence for delta smelt (Bennett 2005). In that study, Bennett (2005) hypothesized that a shrinking volume of physically suitable habitat combined with a high density of competing planktivorous fishes were the primary factors contributing to the decreasing carrying capacity for delta smelt. Our analysis was designed to test the hypothesis that the combined effects of fall stock abundance and fall water quality affect recruit abundance the following summer. We compared eight simple stock–recruit models to evaluate this hypothesis. Comparing the relative fit of models with differing conceptual interpretations is generally superior to simply examining the fit of any single model (Hilborn and Mangel 1997). The abundance indices we used for these models were derived by the California Department of Fish and Game and are available at www.delta.dfg.ca.gov/. Similar to previous studies (Moyle et al. 1992; Bennett 2005), we used the FMWT abundance index as an estimate of fall stock abundance and the Summer Towntnet abundance index as an estimate of summer recruit abundance. The basic model was a simple linear regression of adult stock versus recruit abundance. The other models included fall stock abundance and various combinations of mean annual fall Secchi depth or specific conductance in multiple regressions.

We separated the time series into two segments for this analysis: 1968–1986 and 1987–2004. This separation delineates a major ecological change in the food web of the estuary stemming from the invasion of the clam *Corbula amurensis* (Kimmerer 2002). Intense filtering of the water column by large populations of this clam essentially eliminated phytoplankton blooms in the lower estuary and caused major declines in the abundance of most planktonic invertebrates, including copepods, which are the primary prey of delta smelt (Kimmerer and Orsi 1996; Moyle 2002). Separation of the two time periods allowed us to examine the role of water quality when food was relatively abundant versus when it was not.

We compared the models in each time series by traditional means (level of statistical significance and comparison of r^2 values), but also evaluated the relative fit of each model with an information-theoretic approach based upon Akaike's information criterion (AIC; Burnham and Anderson 1998). This technique allows for a comparison of models with varying numbers of parameters and is based upon a strength-of-evidence context rather than traditional statistical tests of null hypotheses. Candidate models were evaluated based upon AIC, Δ_i , and w_i (Burnham and Anderson 1998): Δ_i (AIC differences) provides a level of empirical support for each model and is evaluated in relative rather than in absolute terms (values of 0–2 provide substantial support for a given model (0 being best), 4–7 considerably less support, and >10 virtually no support); w_i provides a relative weight of evidence in support of a given model with the largest value being best. We further evaluated the fit of the regression models by visually examining residual plots for homogeneity of variance and used the Anderson–Darling test to determine if the residuals were normally distributed.

Table 1. Generalized additive modeling results.

Model	Species		
	Delta smelt (<i>Hypomesus transpacificus</i>)	Striped bass (<i>Morone saxatilis</i>)	Threadfin shad (<i>Dorosoma petenense</i>)
Temperature (T)	11 805 (0.1)	16 542 (0.4)	14 285 (4.4)
Secchi depth (S)	10 295 (12.9)	14 356 (13.6)	14 748 (1.3)
Specific conductance (C)	9 620 (18.6)	14 928 (10.1)	13 066 (12.5)
T + S	10 250 (13.3)	14 290 (14.0)	14 125 (5.4)
T + C	9 537 (19.3)	14 893 (10.3)	12 608 (15.6)
S + C	8 856 (25.1)	13 549 (18.4)	12 874 (13.8)
T + S + C	8 780 (25.7)	13 460 (19.0)	12 387 (17.1)

Note: Residual deviance and percentage of total deviance explained (in parentheses) are given for each model. Null deviance is 11 822 for delta smelt, 16 608 for striped bass, and 14 935 for threadfin shad. The variables in each model were all statistically significant ($P < 0.0001$) based on approximate χ^2 tests.

Results

GAMs

For each species, we found that all three environmental variables were statistically significant predictors of fish occurrence (Table 1). The global model, which included all three water quality variables, accounted for 25.7%, 19.0%, and 17.1% of total deviance in the models for delta smelt, striped bass, and threadfin shad, respectively (Table 1). Relationships between predicted occurrence (based on the global model) and individual water quality variables generally matched our expectations for Secchi depth and specific conductance, but not for water temperature (Fig. 4). Predicted occurrence of each species decreased as Secchi depth increased. Predicted occurrence of striped bass and delta smelt peaked at relatively low values along the specific conductance gradient, whereas for threadfin shad it exhibited a gradual negative relationship. There was no clear trend in the predicted occurrence of striped bass with temperature. For delta smelt, predicted occurrence was highest at the lowest temperature, and for threadfin shad it was highest at the lowest and highest temperatures. The addition of temperature to the GAMs for striped bass and delta smelt did not appreciably improve the amount of the deviance explained (0.4% for striped bass and 0.1% for delta smelt; Table 1). Hence, we concluded that a GAM including Secchi depth and specific conductance was the most appropriate for generating annual EQ trends for further analysis for these species. For threadfin shad, Secchi depth accounted for only 1.3% of the deviance; thus we selected temperature and specific conductance as a final model for threadfin shad.

Trends in EQ

Overall, EQ values were highest for striped bass, intermediate for threadfin shad, and lowest for delta smelt, reflecting both their relative abundance and distributional range in the estuary (Fig. 5). There was an overall negative trend in EQ for each species, with delta smelt and striped bass exhibiting the most apparent declines. The declines in EQ appeared to be most apparent following the mid 1980s. Long-term spatial patterns in EQ (Fig. 6) were generally similar across species in that a high percentage of stations exhibited statistically significant ($P < 0.05$) declines: threadfin shad (64% of stations), delta smelt (63% of stations), and striped bass (65% of stations). There was only one instance

of a station exhibiting a statistically significant increase in EQ; it was near the confluence of the Sacramento and San Joaquin rivers for delta smelt. The western and southeastern regions of the estuary exhibited the most substantial long-term declines in EQ for striped bass and delta smelt, as indicated by consistently steeper negative slopes and statistically significant regressions. The lower Sacramento River exhibited virtually no significant EQ changes for any species. For delta smelt, there were also some nonsignificant regressions for stations in the lower San Joaquin River. The southeastern region of the system exhibited few EQ changes for threadfin shad.

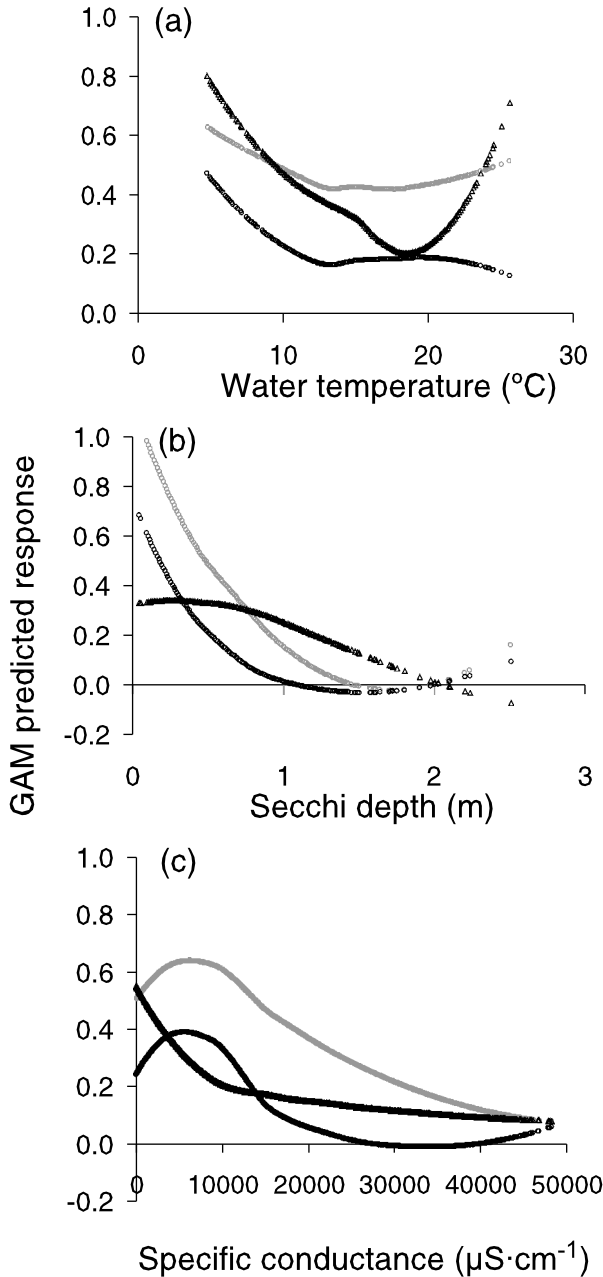
Water quality – delta smelt abundance linkages

The results of the regression modeling support the hypothesis that water quality was an important predictor of delta smelt abundance during the 1987–2004 post-*Corbula* period (Table 2). None of the 1968–1986 pre-*Corbula* regression models were statistically significant ($P > 0.05$). However, all 1987–2004 post-*Corbula* models were statistically significant ($P < 0.02$). The residuals from these significant models were normally distributed (Anderson–Darling P values ≥ 0.05) and exhibited no apparent trend with the fitted values, suggesting the models adequately fit the data. A comparison of the r^2 values suggested that the stock + specific conductance model and the stock + specific conductance + Secchi depth model produced similar results (~60% of variance explained) and were superior in that they accounted for ~30% more variance than the other models. The AIC results also suggested that these two models provided similar fits to the data set and were superior to the other models (Table 2).

Discussion

Understanding fish–habitat relationships is a fundamental step in characterizing EQ, as well as the effects of habitat manipulations on EQ, and ultimately, fish populations. In this study, we used statistical and graphical techniques to establish and evaluate EQ for selected fishes in the San Francisco Estuary. Our ultimate goal was to determine if changes in the water quality variables that defined EQ could have contributed to declines in fish abundance. Our approach was relatively novel in that most similar studies have been of much shorter duration and have been used merely to identify, not further analyze, fish–EQ relationships (Norcross et

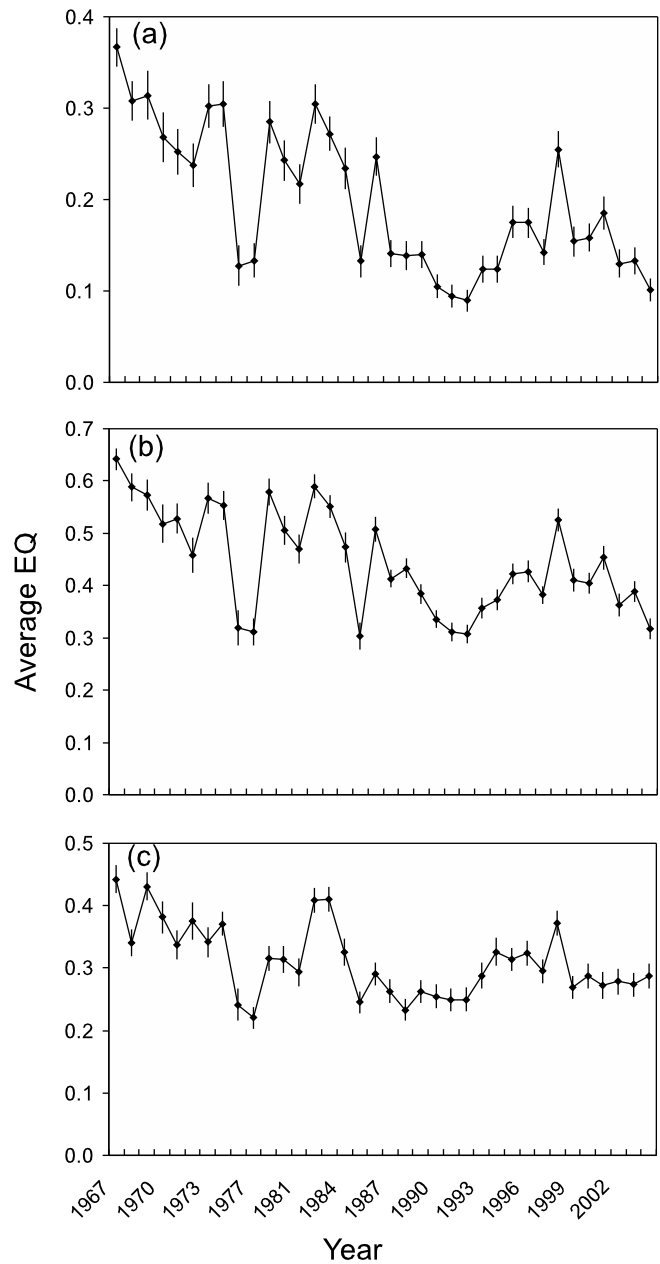
Fig. 4. Generalized additive model (GAM) predictions of fish occurrence (based on all three water quality variables) versus the observed individual water quality parameters ((a) water temperature, (b) Secchi depth, (c) specific conductance) for threadfin shad (*Dorosoma petenense*) (black triangles), delta smelt (*Hypomesus transpacificus*) (black circles), and striped bass (*Morone saxatilis*) (gray circles).



al. 1997; Stoner et al. 2001). Whereas these previous studies sometimes used GAM results to make inferences about the likelihood of fish occurrence at new or unsampled locations, the extensive temporal (36 years) and spatial (100 stations) coverage of the FMWT survey afforded us an unusual opportunity to examine multidecadal trends throughout the estuary and in multiple geographic locations.

The first objective in our study was to relate fish occurrence to water quality variables to establish EQ for the three

Fig. 5. Environmental quality (EQ) time series for threadfin shad (*Dorosoma petenense*), delta smelt (*Hypomesus transpacificus*), and striped bass (*Morone saxatilis*). The average and variation based on two standard errors are shown for each species.



investigated species. We found that Secchi depth and specific conductance were important factors explaining the occurrence of delta smelt and striped bass, while specific conductance and water temperature were important for threadfin shad. Our GAMs using all three variables reduced null deviance between 17% and 26%, levels comparable with other studies (Maravelias 1999; Stoner et al. 2001). The GAM analysis results are consistent with information about the life history of each species. Delta smelt and age-0 striped bass are low-salinity zone specialists (Turner and Chadwick 1972; Moyle et al. 1992), and threadfin shad are mostly confined to freshwater zones, so it is reasonable to expect specific conductance to affect their occurrence. For delta smelt,

Fig. 6. Spatial distribution of long-term trends in annual environmental quality (EQ) for (a) delta smelt (*Hypomesus transpacificus*), (b) threadfin shad (*Dorosoma petenense*), (c) striped bass (*Morone saxatilis*) in San Francisco Estuary shown for the region bordered downstream at Carquinez Strait. Color shading represents the coefficient for the year term for individual linear regressions of EQ versus year for each station. Lighter shading represents a more negative slope. Open circles and solid circles represent stations with nonsignificant ($P \geq 0.05$) or significant regressions ($P < 0.05$), respectively.

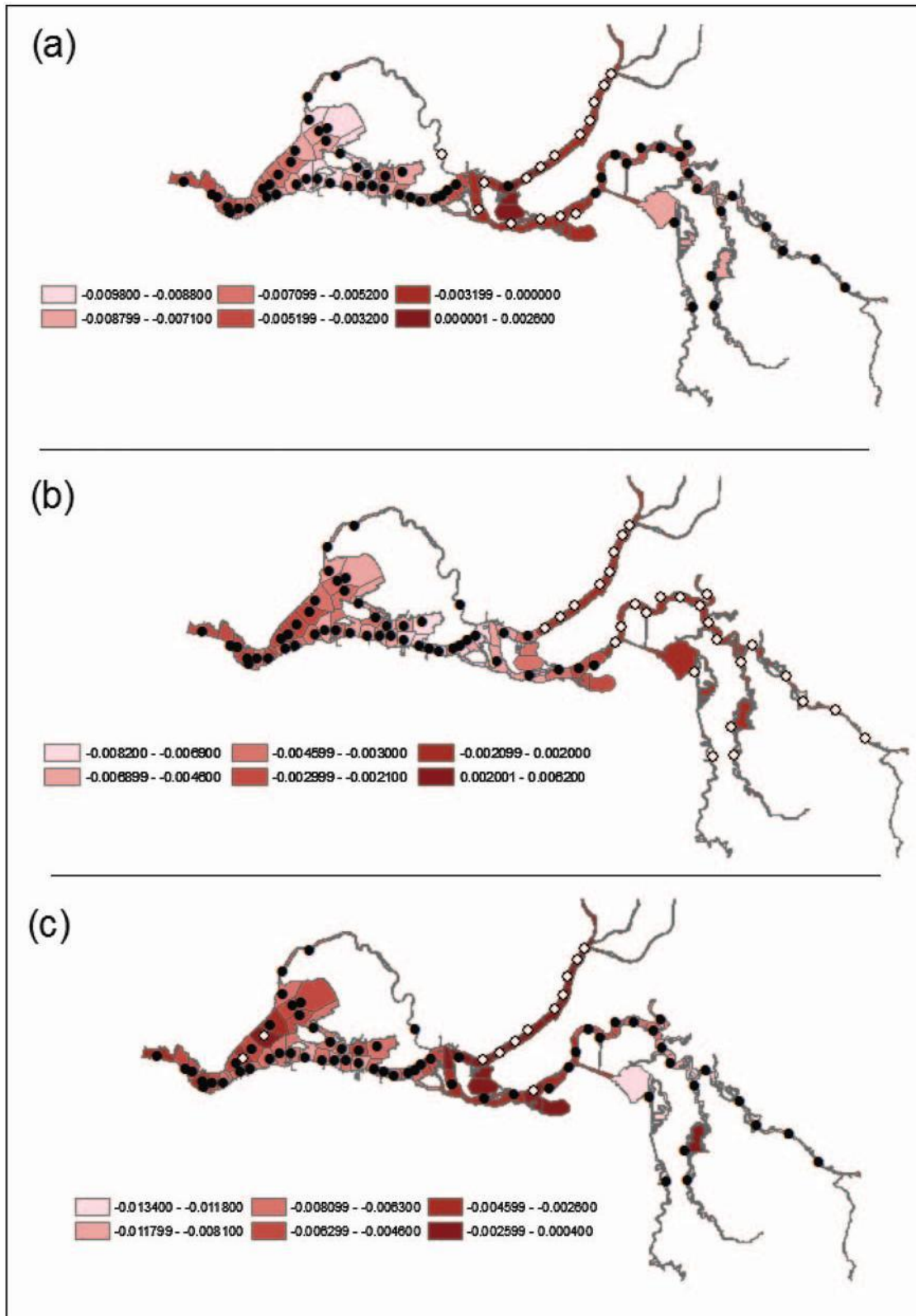


Table 2. Regression statistics for various stock–recruit models for delta smelt (*Hypomesus transpacificus*) for the 1987–2004 post-*Corbula* time period.

Fall stock	Specific conductance	Secchi	Constant	df	<i>P</i>	<i>r</i> ²	AIC	Δ_i	<i>w</i> _{<i>i</i>}
0.0078	—	—	1.5	16	0.005	39.5	96.08	6.0	0.003
0.0067	−0.00068	—	12.3	15	0.001	59.6	90.08	0.0	0.06
0.0076	—	−7.9	6.7	15	0.018	41.6	97.4	7.3	0.002
0.0068	−0.00069	1.6	11.5	14	0.0004	59.6	92.8	2.7	0.02

Note: The same models were developed for the 1968–1986 pre-*Corbula* time period but are not shown because none were statistically significant ($P > 0.05$). The dependent variable for all regression models was the delta smelt recruit abundance index, as measured by the Summer Townet Survey. Candidate models were developed based on the possible combinations of the fall stock abundance index, with average fall values of specific conductance and Secchi depth as independent variables. Akaike's information criterion (AIC), AIC differences (Δ_i), and AIC weights (w_i) are also shown.

our results are consistent with laboratory studies on their physiological tolerances to salinity (Swanson et al. 2000). Because delta smelt require turbidity for successful feeding (Baskerville-Bridges et al. 2004) and because predation is mediated by turbidity, it is possible that long-term increases in Secchi depth may have affected feeding success and predation pressures.

Factors affecting fish distribution often interact along spatial and temporal gradients (Jackson et al. 2001). Thus, it is critical to understand their spatiotemporal trends (study objective 2). The long-term EQ trends showed similar declines for each species across a broad geographical range. However, the steepest declines and highest levels of statistical significance occurred in the western, eastern, and southern regions. These results suggest that the lower Sacramento River has exhibited the least long-term habitat alteration as compared with the rest of the estuary, at least with respect to the evaluated abiotic factors. For delta smelt, there was some evidence that EQ had not declined as substantially in the lower San Joaquin River, suggesting that EQ in the region just upstream of the confluence of the Sacramento and San Joaquin rivers has remained relatively stable for delta smelt.

The spatial and temporal trends in EQ can largely be explained by an interaction of climate variability and anthropogenic factors. The increase in Secchi depth during the study period is primarily a function of a decline in total suspended solids, one of the long-term effects of upstream dam construction (Jassby et al. 2002). Wright and Schoellhamer (2004) documented that sediment transport to the estuary from the Sacramento River has declined by 50% since 1957. Nobriga et al. (2005) hypothesized that this change in sediment dynamics and corresponding changes in hydrodynamics have had dramatic effects on fish assemblages and the proliferation of alien fishes in the system. In addition, Nobriga et al. (2005) observed that submerged aquatic vegetation, especially the invasive Brazilian waterweed (*Egeria densa*), became increasingly abundant in the system during the past 20 years. This macrophyte increases water clarity by trapping suspended sediments and also has had measurable effects on the fish community. The increase in specific conductance during the study period is likely a function of decreasing river flow entering the estuary during the fall. There has been no significant long-term trend in runoff entering the watershed of the estuary during September–December (Dettinger and Cayan 1995). Thus, the positive specific con-

ductance trend appears to be the result of water operations; the change could be a consequence of less water released from upstream dams into the system during this time of the year, or more water exported from the south delta, or a combination of both effects.

The third objective of our study was to determine if changes in water quality could explain the observed declines in the abundance of delta smelt, an annual fish species. The simple statistical models evaluated for delta smelt suggest that water quality may indeed be an important factor, at least during the past two decades, when food availability was severely reduced by the invasion of *Corbula*. This finding is consistent with previous analyses on population dynamics of delta smelt and striped bass, which revealed long-term declines in carrying capacity (Kimmerer et al. 2000; Bennett 2005). A decline in suitable physical habitat and decreases in prey availability are two of the likely mechanisms for the changes in carrying capacity. Studies on the physiological tolerances of delta smelt suggest that they can survive in salinities higher than those at which they have been found in the wild (Swanson et al. 2000). This suggests that recent patterns of fish recruitment and abundance are probably controlled by multiple interacting factors. Current efforts in parameterizing life cycle models for delta smelt and striped bass are likely to better quantify the relative importance of water quality on their population dynamics.

Although we believe that our results are robust given the substantial amount of data, we acknowledge that our analysis did not include all potential water quality, physical, or biological factors that affect fish occurrence and habitat. With respect to water quality, dissolved oxygen is perhaps the most important variable that we could not evaluate because of a lack of suitable data. Dissolved oxygen requirements for delta smelt are poorly understood; however, both striped bass and threadfin shad are sensitive to low levels of dissolved oxygen (Moyle 2002). In general, dissolved oxygen levels are not a major problem in most regions of the San Francisco Estuary. Problem areas include the extreme upstream limits of the south Delta during summer and fall (Lehman et al. 2004) and in the sloughs of Suisun Marsh during fall drainage of reclaimed marshlands (P. Moyle, University of California – Davis, Wildlife, Fish and Conservation Biology, Davis, California 95616, USA, personal communication). Both of these regions are outside of the sampling area covered by the FMWT.

Physical habitat features such as substrate type (e.g., sand, mud, detritus, etc.), depth (e.g., shoals versus channels), and cover (e.g., woody debris or submerged aquatic vegetation) can also be important variables for fish habitat. Although data of this type are relatively scarce for fishes in San Francisco Estuary, we have no reason to believe that there have been major changes in these variables except for vegetative cover. As noted previously, there have been substantial increases in the amount of submerged aquatic vegetation during the past 20 years (Nobriga et al. 2005). We evaluated the increase in Secchi depth, one of the potential effects of this invasion, but were not able to analyze the effects of the increase in physical structure in the estuary.

Biotic variables, most notably competition, predation, and food availability, could have also played a major role in controlling the distribution of the three fishes (Hayes et al. 1996). Including competition in explanatory models would be extremely difficult in a practical sense because it is complicated to measure and is affected by many other variables. There have been some limited diet studies of piscivorous fishes in the estuary (e.g., Turner and Kelly 1966; Feyrer et al. 2003; Nobriga et al. 2006); however, the bioenergetics of predation within the estuary have remained largely unmeasured or modeled (but see Lindley and Mohr 2003 for a paper modeling striped bass predation on winter-run Chinook salmon (*Oncorhynchus tshawytscha*)).

Perhaps the greatest opportunity for improving our analyses of EQ distributions and trends lies with additional studies on the effects of food availability. Food availability has been successfully incorporated into similar GAMs (Maravelias 1999; Stoner et al. 2001). Moreover, some work in San Francisco Estuary suggests that prey availability can affect fish populations, especially striped bass (Kimmerer et al. 2000, 2001; Feyrer et al. 2003) and delta smelt (Bennett 2005). Although we did not include a direct measure of food availability in our models because there were no comparable invertebrate data at the spatial and temporal resolution of the FMWT data, our comparison of stock–recruit models for delta smelt suggests that food availability plays an important role.

We also acknowledge that our study is focused on conditions during a single season of the year, but it represents 1/3 of a year. Conditions during other seasons undoubtedly play a role in the population dynamics of the fish species we examined, but the changing physical habitat conditions during fall are likely important for several reasons. For age-0 striped bass, conditions during their first autumn play a role in the density-dependent survival exhibited by this species from age-0 to age-3 (Kimmerer et al. 2000). This is especially true given that food web changes have affected diet composition (Feyrer et al. 2003). Fall conditions may be even more important for delta smelt and threadfin shad, since these fish represent prespawning adults. In general, less suitable habitat constricts the range of these fishes, which combined with an altered food web, may affect their health and survival.

Overall, our study illustrates that ecological knowledge gained from long-term monitoring data can be a valuable tool to understand changes in aquatic ecosystems. First, they highlight the utility of long-term data sets to describe fish–

EQ relationships, derive EQ, and track EQ trends for a variety of species. The long-term declining EQ trends and the apparent link to delta smelt abundance detected in this study corroborate previous hypotheses that the area of suitable physical and chemical habitat has played a role in the decline in fish abundance. However, the degree to which EQ could be used for management purposes remains unclear. Flow standards in San Francisco Estuary are based largely on a surrogate for salinity (X_2), particularly during winter and spring. While X_2 is a valuable generalized variable that is relatively easy to measure and is correlated with long-term abundance trends of multiple species (Jassby et al. 1995; Kimmerer 2002), the recent step change in the abundance of pelagic fishes suggests that salinity alone may not be sufficient to explain long-term trends in estuarine management. Our analyses of EQ showed that water transparency might also be an important consideration. For example, the combined effects of specific conductance and Secchi depth improved the stock–recruitment relationship for delta smelt, a species that has proven difficult to model using a variety of environmental data (Bennett 2005). Nonetheless, it is questionable whether there are simple ways to use variables such as Secchi depth for species management, at least during the fall period that we studied. Moreover, for the water quality data to be most effective for species management, additional information is needed to better define the mechanisms for the effects of water quality variables on aquatic organisms.

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