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Is the Response of Estuarine Nekton to Freshwater Flow in the San Francisco Estuary Explained by Variation in Habitat Volume?

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Abstract Abundance of estuarine biota can vary with freshwater inflow through several mechanisms. One proposed mechanism is that the extent of physical habitat for an estuarine species increases with flow. We estimated the contribution of variation in habitat volume to the responses of eight species of estuarine nekton to changes in freshwater flow in the San Francisco Estuary. Resource selection functions for salinity and depth were developed for each species (and for five additional species) using five monitoring data sets. The TRIM3D hydrodynamic model was run for five steady flow scenarios to determine volume by salinity and depth, and resource selection functions were used as a weighting factor to calculate an index of total habitat for each species at each flow. The slopes of these habitat indices vs. flow were consistent with slopes of abundance vs. flow for only two of the species examined. Therefore, other mechanisms must underlie responses of abundance to flow for most species.

Keywords Fish · Habitat · Freshwater flow · Resource selection function · San Francisco Estuary

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Introduction

Variability in freshwater flow is the principal mode of interannual and seasonal variation of physical conditions in many estuaries (Skreslet 1986). River discharge into estuaries may be sensitive to climate change and increasing human demand (Vörösmarty et al. 2000; Scavia et al. 2002). Thus, understanding mechanisms by which estuarine ecosystems respond to freshwater flow should yield important insights into the dynamics of these ecosystems and their sensitivity to perturbation.

Biological populations in estuaries often vary with freshwater flow. Positive flow effects have been reported for phytoplankton production (Riley 1937; Mallin et al. 1993; Sin et al. 1999) and for abundance or harvest of benthic invertebrates (Aleem 1972; Gammelsrød 1992; Montagna and Kalke 1992; Wilber 1992, 1994; Reaugh et al. 2007) and fish (Stevens 1977; Houde and Rutherford 1993; Jassby et al. 1995). Negative effects on biological populations can also occur (Rose and Summers 1992), e.g., through effects of washout or osmotic stress (Deegan 1990; Kaartvedt and Aksnes 1992).

Various potential mechanisms have been proposed for positive effects of freshwater flow on biological populations (e.g., Nixon et al. 1986; Cloern 1991; Drinkwater and Frank 1994; Kimmerer 2002a, b). One proposed mechanism is the increase in area or volume of physical habitat for biota that accompanies increases in freshwater flow (mechanism no. 10, Kimmerer 2002b). This mechanism may explain increases in the abundance of Sacramento splittail, *Pogonichthys macrolepidotus*, with freshwater flow in the upper San Francisco estuary (Sommer et al. 1997). When high flow inundates floodplains adjacent to the estuary, splittail gain access to large areas of habitat, particularly for foraging and spawning (Feyrer et al. 2006).

Chinook salmon may also benefit from inundated floodplains through increased foraging opportunities (Sommer et al. 2005). For species not dependent on floodplains, there is little evidence for or against this mechanism.

In this paper, we determine how the quantity of habitat for estuarine nekton, defined by salinity and water depth, responds to changes in freshwater flow in the San Francisco Estuary and the extent to which species-specific habitat responses translate to flow responses. Salinity is a key attribute of the habitat of all estuarine species (Fig. 35 in Kimmerer 2004), and water depth is likely important for some, particularly demersal, species. Furthermore, the isohalines move in response to freshwater flow, so that the joint salinity–depth distribution varies with flow.

We follow Jassby et al. (1995) and Kimmerer (2002a, b) in using X_2, the distance up the axis of the estuary to the daily averaged near-bottom 2-psu isohaline, as a measure of the physical response of the San Francisco Estuary to flow. Using this variable rather than flow itself incorporates the natural response time of the estuary to changes in flow and provides a geographic scale that is easy to interpret. Previously, the relationships of annual abundance or survival indices of several fish and shrimp species have been related to X_2 (Jassby et al. 1995).

Hydrodynamic modeling and analysis of abundance and distribution data were used to determine the relationship between extent of physical habitat and flow. Our general approach was (1) to calculate resource selection functions (Manly et al. 2002) from monitoring data as measures of habitat use, (2) to estimate habitat volume using a hydrodynamic model, (3) to calculate habitat indices by combining habitat use and habitat volume, (4) to relate these habitat indices to X_2, and (5) to compare these relationships with the abundance–X_2 relationships. The latter relationships were also updated with recent data and calculated for additional sampling programs and additional species beyond those used originally (Jassby et al. 1995; Kimmerer 2002a, b).

Materials and Methods

Study Area The San Francisco Estuary (Fig. 1) is a large estuary with a river-dominated northern branch and a lagoonal southern branch (Nichols et al. 1986). Numerous publications including several compendia describe its geography, climate, physical oceanography, chemistry, and ecology (e.g., Conomos 1979; Cloern and Nichols 1985; Hollibaugh 1996; Kimmerer 2004). Tectonically shaped topography divides the estuary into a series of basins separated by narrow deep channels. The easternmost region of the estuary is the delta of the Sacramento and San Joaquin Rivers, a complex network of tidal channels around leveed islands.

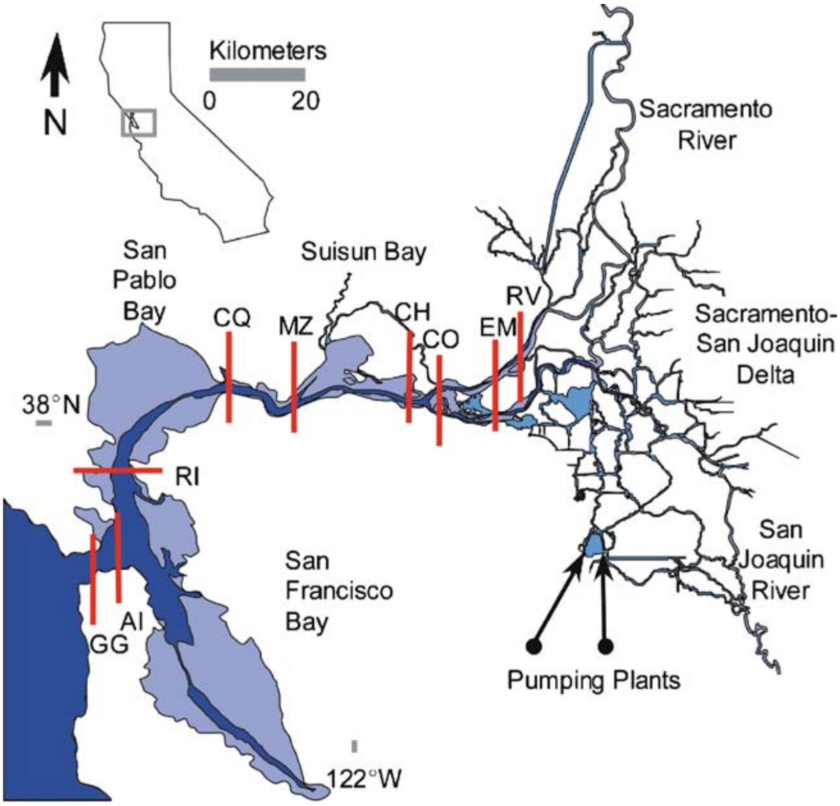


Fig. 1 Map of the San Francisco Estuary showing major basins and the 10-m depth contour. *Lines with pairs of letters* indicate cross-sections shown in TRIM3D model output of salinity profiles (Fig. 6). *GG* Golden Gate Bridge, *AI* Angel Island, *RI* Richmond Bridge, *CQ* Carquinez Bridge, *MZ* Martinez, *CH* Chipps Island, *CO* Collinsville, *EM* Emmaton, *RV* Rio Vista

Central California's climate is Mediterranean, with a winter wet season and a summer dry season. Freshwater input to the estuary is highly variable on all timescales (Nichols et al. 1986). The estuary drains about 40% of the area of California and its watershed supplies water for most of the state's agriculture and for some 22 million residents. Much of that water is stored in reservoirs to the north, then released during the summer dry season and pumped from the Delta to the south (Fig. 1). Environmental conflicts arising from this practice have led to many restrictions on pumping and to the availability of funds for extensive monitoring and research programs.

Data Sources X_2 was initially determined through interpolation of salinity between sampling stations. Since 1992, X_2 has been estimated using a time series regression on freshwater outflow (Jassby et al. 1995). Outflow was obtained from the California Department of Water Resources' Dayflow accounting program (http://www.iep.ca.gov/dayflow/). Catch data and abundance indices for nine common species were obtained from five data sets from four sampling programs (Table 1). Northern anchovy, not in the original analyses, was added to this list because of its high abundance in the estuary. All data were for young-of-the-year (YOY), except for starry flounder which was collected most effectively as age-1 fish. Data from the first four sources in Table 1 were used both for updating the abundance–X_2 relationships and calculating habitat use. Data from the spring–summer 20 mm survey were used only to calculate habitat use, since abundance indices are not determined from that data set.

The summer townet survey (TNS; Turner and Chadwick 1972) sampled two to five times annually during 1959–2007 (except 1966) at approximately 2-week intervals starting in June and ending when the mean size of striped bass exceeded 38 mm. Triplicate tows were taken throughout the northern estuary at a median of 27 stations. The striped bass YOY index was calculated as in Turner and Chadwick (1972) from the catch of young striped bass during the last two sample surveys of each year. The TNS index for delta smelt was calculated from the mean catch in the last two surveys.

The fall midwater trawl program (MWT) obtained data during 1967–2007 (except 1974 and 1979), monthly from September to December, at a median of 88 stations throughout the northern estuary (Moyle et al. 1992). The mean catch per tow in each month was calculated for each of 17 regions and multiplied by the volume in that region, then summed over the 4 months to obtain an abundance index.

The San Francisco Bay study (Armor and Herrgesell 1985) took samples monthly all year during 1980–2007, except in winter months in some years. Single tows were taken at 45 stations (median) throughout the estuary using both a midwater trawl of the same design as that used in the fall survey (Bay MWT) and an otter trawl (Bay OT). Abundance indices were calculated similarly to those from the fall midwater trawl program using the otter trawl for demersal species and the midwater trawl for other species.

The spring–summer 20 mm survey was designed to capture late larvae and juveniles of delta smelt (Dege and Brown 2004). Triplicate tows were taken in eight to nine surveys between March–April and July–August during 1995–2006 at a median of 41 stations throughout the northern estuary.

Abundance–X_2 Relationships Analyses of relationships of abundance to X_2 followed previous approaches (Kimmerer 2002a) but with a broader suite of response variables, including indices from more than one sampling program and for six additional species (the freshwater threadfin shad *Dorosoma petenense* and five marine species: bay goby *Lepidogobius lepidus*, English sole *Pleuronectes vetulus*, Pacific sanddab *Citharichthys sordidus*, shiner surfperch *Cymatogaster aggregata*, and staghorn sculpin *Leptocottus armatus*). The log of the annual abundance index was related to X_2 averaged over several spring months when each species is likely to be most vulnerable to freshwater flow effects. The X_2 values for age-1 starry flounder were lagged 1 year. Relationships for most species included a step change in 1987 to allow for the possibility of an effect of declining food supply due to grazing by the introduced clam *Corbula amurensis* (Kimmerer 2002a). More recently, some of the species included in those analyses have suffered further declines (Sommer et al. 2007). For delta smelt in the summer townet survey, the slope changed in 1981–1982 so that step was included in the model as an interaction term, and the 1987 step was omitted.

Young striped bass were treated slightly differently to account for strong effects of stock size on production of young. Abundance indices from each of the sampling programs were used as for other species, but were limited to data after 1977 (summer and fall surveys only) because of the substantial decline in YOY caused by the large drop in egg production in 1976–1977 (Kimmerer et al. 2000). We also used survival from egg to the first summer as a response variable, estimated as described in Kimmerer (2002a). Egg production was calculated from age-specific fecundity and adult abundance by age as determined by Petersen estimates from mark-recapture studies (Kimmerer et al. 2000). Summer abundance was the mean catch per trawl in the summer townet survey, which is closely correlated with the townet index used previously (r=0.95 between annual values) but is based on more samples. Adult striped bass were sampled in all years from 1967 through 1994 but only during even years between 1994 and

Table 1 Species included in the abundance–X_2 or habitat analyses, with relevant life history information

Taxon	Abbrev.	Life history information	Source for habitat analysis				
			TNS	MWT	Bay MWT	Bay OT	20 mm
Bay shrimp *Crangon franciscorum*	BS	Adults spawn in lower estuary or coastal ocean, young move into the estuary in spring to rear in shallow areas (Hatfield 1985).				6,518 (May–Nov)	
Starry flounder *Platichthys stellatus*	SF	Adults spawn in winter in lower estuary or coastal ocean, larvae and juveniles move far into the estuary in spring to rear (Emmett et al. 1991).				10,820 (All year)	
Pacific herring *Clupea pallasi*	PH	Adults migrate from ocean to lower estuary in winter to spawn; larvae rear in estuary (Emmett et al. 1991).					12,887
American shad *Alosa sapidissima*	AS	Anadromous, adults spawn in spring, larvae and juveniles rear in estuary (Emmett et al. 1991).		13,697	4,856 (May–Nov)		
Delta smelt *Hypomesus transpacificus*	DS	Adults spawn in late winter–spring, larvae and juveniles rear near Low-Salinity Zone (Bennett 2005).	6,452	13,697			12,887
Longfin smelt *Spirinchus thaleichthys*	LS	Adults spawn at age 2 in late winter, larvae rear near Low-Salinity Zone, juveniles further seaward (Rosenfield and Baxter 2007).	6,452	13,697	7,777 (May–Dec)		12,887
Sacramento splittail *Pogonichthys macrolepidotus*	SS	Adults spawn in early spring on flood plains. Juveniles rear in fresh to brackish water (Sommer et al. 1997).		13,697			
Striped bass *Morone saxatilis*	SB	Adults spawn in rivers in spring, larvae and juveniles rear in Low-Salinity Zone (Turner and Chadwick 1972).	6,452	13,697	7,777 (May–Dec)	7,225 (May–Dec)	12,887
Northern anchovy *Engraulis mordax*	NA	Coastal population also resident in estuary (Kimmerer 2006)		13,697	8,065 (Apr–Nov)		

Species include northern anchovy, not in the original analyses (Kimmerer 2002a), and Sacramento splittail, which was in the original analyses but for which habitat analyses were not conducted. Source columns give the number of samples for each survey and each species used in the habitat analyses: TNS, summer townet survey; MWT, fall midwater trawl survey; Bay MWT, San Francisco Bay Study midwater trawl, and Bay OT, San Francisco Bay Study otter trawl; 20 mm, spring–summer survey of juvenile fish. Time periods given for the Bay Study samples indicate the periods of high abundance used in analysis of each species; all data were used in other surveys because they were limited to relatively brief periods

2004, and abundance estimates are not yet available for 2006–2007. We filled in missing values by interpolation (level extrapolation for the last 2 years) for graphs only, but excluded these values from statistical analyses. A step change in the abundance–X_2 and survival–X_2 relationships occurred in 1995–1996 based on a regression tree on the residuals from a linear regression, so only that year had a step change in the final models for striped bass.

Habitat Indices We developed habitat indices by combining resource selection functions (Manly et al. 2002) that describe habitat use with estimates of habitat volume. Analyses were completed for eight of the nine species in Table 1. Sacramento splittail was excluded from this analysis because its spawning and rearing habitat is outside the domain of the hydrodynamic model used to determine habitat volume. Other abundant species found almost entirely in freshwater (e.g., threadfin shad) were excluded for the same reason.

For a given species and sampling program:

$$H(Q) \propto \sum_{All\,S} \sum_{All\,Z} h(S,Z) V_{S,Z}(Q) \qquad (1)$$

where H is an index of habitat quantity as a function of freshwater flow Q, h is a discrete or continuous resource selection function of salinity and water depth, and $V_{S,\,Z}\,(Q)$ is the volume of water in a given range of salinity S and water depth Z as a function of flow. The resource selection function h was based either on catch per trawl or frequency of occurrence. In this discrete formulation of H, salinity is divided into blocks of one unit (i.e., 0–1, 1–2, etc.) and depth in blocks of 1 m in the top 20 and 5 m below 20 m. The index H is taken as proportional to the sums on the right of Eq. 1 because the resource selection function h includes an arbitrary scaling factor (Manly et al. 2002).

Resource Selection Functions We calculated functions h for common species using raw catch data from all four sampling programs (five data sets). We selected all samples for which catch and salinity data were available (Table 1). For the San Francisco Bay study, we also selected time periods when the target life stage of each species was abundant (Table 1); this was unnecessary for the other surveys because their durations were more limited.

A wide variety of methods is available for examining habitat use, and the choice among them is not necessarily statistically based (Guisan and Zimmermann 2000). We selected generalized additive models (GAMs) to fit catch per trawl and frequency of occurrence to salinity and (in some cases) depth (Swartzman et al. 1992; Maravelias 1999; Stoner et al. 2001; Feyrer et al. 2007). GAMs extend the applicability of linear models by fitting relationships after smoothing the independent variables (Venables and Ripley 2002). Thus, they can represent curved relationships without the need to determine and understand the underlying function, and residuals can have non-normal error distributions. These curved relationships capture at least some measure of habitat quality in that catches of fish should generally be reduced in low-quality habitat.

We applied a binomial error distribution to frequency of occurrence and a Poisson error distribution to catch per trawl. We used a locally weighted regression (loess) as the smoother (Swartzman et al. 1992) for salinity and a linear fit for depth when it was included. The loess smoother parameters were degree=2, meaning a quadratic local fit, and span=0.5, meaning a sampling window equal to half of the range of salinity. Resource selection functions generally fit the data better with a shorter span parameter, but at the expense of excessive small-scale fluctuation, and spans of 0.25–0.75 gave essentially the same results. Exploratory analyses were used to examine the importance of water depth and Secchi depth as predictor variables. Because of the large number of data points in each analysis (Table 1), statistical significance was not a useful criterion for including a term in a model. Therefore, these analyses generally relied on graphical comparisons of models and on approximate coefficients of determination calculated as

$$1 - \frac{D_{res}}{D_{tot}} \qquad (2)$$

where D_{res} is residual deviance and D_{tot} is total deviance (Venables and Ripley 2002). Depth was included in the habitat analysis only if it increased the approximate coefficient of determination by at least 5%.

Generally, depth was important for the Bay Study otter trawl and for some species in other sampling programs. Only the Bay Study sampling covered most of the joint range of depth and salinity. The other surveys had relatively few deep stations and relatively little coverage at high salinity because of their more limited geographic range. Therefore, depth was included in analyses of data from the Bay Study otter trawl but not in others.

GAM analyses were run using all of the data from each sampling program and then using 25 bootstrapped samples of each data set to determine approximate confidence limits around each of the resource selection functions. The h values corresponding to the original data and to each of the bootstrap samples were used to calculate H, and confidence limits were determined using t=2.06, corresponding to 24 degrees of freedom. All analyses were conducted in S-Plus (Venables and Ripley 2002).

Habitat Volume The volume of habitat in each block of depth and salinity was determined using the TRIM hydrodynamic model (Casulli 1990; Cheng et al. 1993; Casulli and Cattani 1994). The TRIM model has been applied extensively to simulate hydrodynamics of the San Francisco Estuary in both depth-averaged (TRIM2D) and three-dimensional versions (TRIM3D). The three-dimensional version applied here was set up specifically for this purpose and represented all of the estuary through the western Delta using a grid of 200×200 m by 1-m-deep cells (Fig. 2). Because the bathymetric variability of many Delta channels cannot be resolved at this scale and increasing resolution would exact a large penalty in run time, most of the Delta was represented as a pair of basins tuned to provide approximately correct tidal flows at the western margin of the Delta. This limits the analysis to species in brackish to saline water during the life stages being examined.

The model was calibrated to an extensive data set including water level and salinity from continuous monitoring stations and discrete samples from the highly variable period of January 1997 to April 1998 and was validated using data from the dry period in 1994 (Gross et al. 2006, Gross et al., in review). Modeled salinity was correlated with data from 14 continuous monitoring sensors with correlation coefficients of 0.90 to 0.99, and the largest mean error in salinity was 1.8 at the bottom sensor in central Suisun Bay (Fig. 1).

The model was run to steady state in five flow scenarios, with freshwater flow into the estuary at 110, 260, 630, 1200, and 2,810 $m^3 s^{-1}$. We used a repeating daily tide comprising the M2 tidal component modified to a 12-h period and the K1 tidal component modified to 24 h, thereby avoiding the need to average over the spring–neap tidal cycle. X_2 values corresponding to each flow level were calculated using the daily time series equation in Jassby et al. (1995).

A table of habitat volumes was constructed for each flow value, using salinity and depth produced by the TRIM3D model. First, daily mean salinity was calculated for each grid cell and averaged over the water column. Bottom salinity was used for the Bay Study otter trawl data. Tables of $V_{S,\ Z}$ were constructed by summing the volumes of all model grid cells with mean salinity within each one-unit increment and total water column depth below the National Geodetic Vertical Datum (roughly mean sea level) within each 1- or 5-m depth increment. The portion of the Delta not resolved by the model was assumed to have a constant depth of 6 m and to be entirely freshwater.

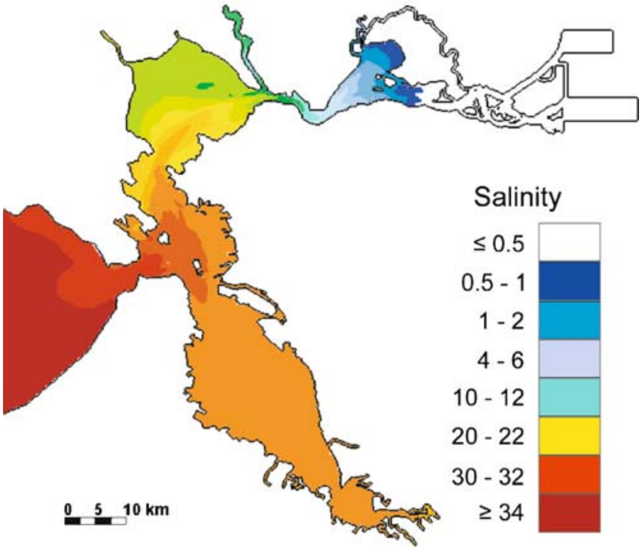


Fig. 2 Domain and grid of the TRIM3D model showing water column mean salinity for a steady-state run with moderate freshwater flow of 630 $m^3 s^{-1}$

We repeated the calculations of H for each resource selection function using bottom salinity instead of the water column mean, except for the Bay Study otter trawl data. Correlations between H values based on bottom salinity and those based on water column means were all >0.94 and most were >0.99. We also repeated the analyses using habitat area instead of volume and found that slopes of habitat volume vs. X_2 were correlated with slopes of habitat area vs. X_2 at $r \geq 0.97$. In other words, for each data set, habitat area and volume gave essentially the same result. The remaining analyses of these data were conducted using the water column mean salinity (bottom salinity for the Bay Study otter trawl data) and volume rather than area.

Slopes of regressions of log H on X_2 were compared with the slopes of log abundance or survival vs. X_2. The assumption was that the two slopes for a given species would be similar if variation in habitat with X_2 were a substantial contributor to the relationship of abundance to X_2 for that species. Using log-transformed dependent variables eliminated differences in scaling of the two kinds of variables.

Results

The updated abundance–X_2 relationships, which include step changes during single years as described above (Fig. 3 and Table 2), were similar to those previously published (Jassby et al. 1995; Kimmerer 2002a). One exception is for Pacific herring: the updated X_2 relationship for the abundance index was flat and that for the egg-young survival index (not shown) was also flat. Abundance–X_2 relationships were consistent among the various sampling programs for all species except delta smelt. The X_2 relationship for delta smelt in the summer townet survey had a step change in slope in 1981 (Fig. 3e), but the midwater trawl survey had an essentially flat relationship with X_2 and a step change in intercept in 1987–1988. Species not included in the previous analyses had no significant X_2 relationships (the last six species in Table 2).

Fits of the GAMs including both salinity and depth gave approximate coefficients of determination between 5% and 52% for catch per trawl and 4% and 45% for frequency of

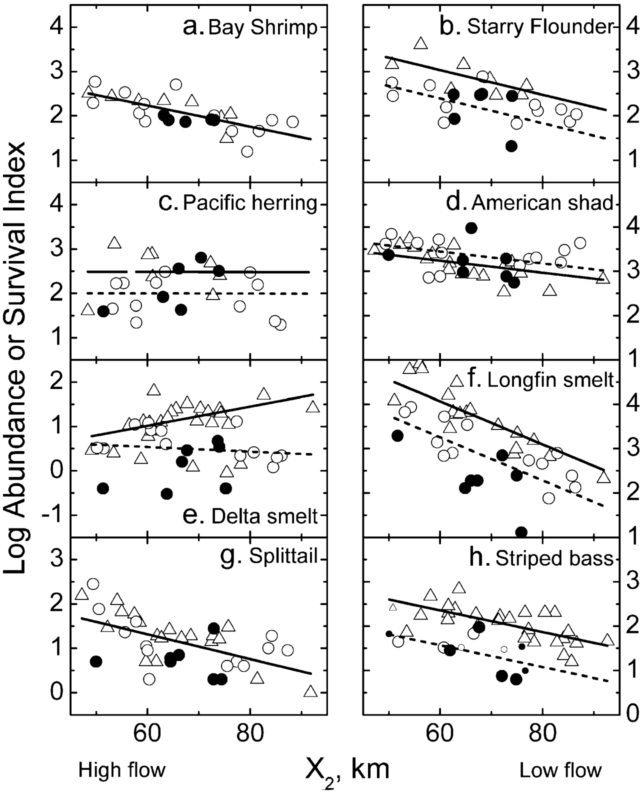


Fig. 3 Log_{10} abundance indices for fish and shrimp (survival index for striped bass) plotted against X_2 as in Kimmerer (2002a, b, Fig. 8a). *Symbols* show data from three periods of generally consistent responses: *triangles and solid lines*, data up to 1987; *circles and dotted lines*, 1988–2006; *filled circles*, 2000–2007 (bay shrimp through 2006 only). *Small symbols* for striped bass based on interpolated or extrapolated egg production, not used in analysis. *Lines* drawn only when statistically significant. See Table 2 for regression statistics

occurrence (Table 3). The low coefficients of determination are largely a function of the huge variability among samples even within the same salinity range (Fig. 4). Excluding depth from the analyses reduced the coefficients of variation by 0% to 22% with medians of 4% and 2% for catch per trawl and frequency of occurrence, respectively. Adding log of Secchi depth as a covariate improved the fit substantially for some species, as demonstrated by the increased coefficients of determination (e.g., delta smelt, longfin smelt, and striped bass; Table 3).

For some species, the habitat curves based on catch per trawl gave tighter responses to salinity than did those based on frequency of occurrence (Fig. 4) because high frequencies of occurrence can be associated with both high and moderate catch per trawl. Simulations based on specified underlying distributions with respect to salinity (not shown) confirmed that habitat curves based on catch per trawl were usually closer to the underlying distributions than those based on frequency of occurrence, which tended to have fat tails.

Bootstrap replicates generally had similar shapes to the resource selection functions calculated with the original data, but variable peak values (Fig. 4). Differences were more pronounced with catch per trawl than with frequency of occurrence because of the influence of occasional very high values. These differences had relatively minor effects on the calculated values of H or the slopes of $\log(H)$ with X_2.

The entire set of resource selection functions showed reasonable consistency among the different sampling programs and large differences among species (Fig. 5). The principal exception to the consistency among sampling programs was for longfin smelt, which had a peak resource value at salinity near 20 in the Bay Study otter trawl but near 10 or less in the other samples (Fig. 5f). This is apparently due to a shallower depth distribution of the longfin smelt when in more landward locations and a movement to deeper water when more seaward (at higher salinity).

Output of the TRIM3D model (Fig. 2) showed progressively seaward movement of the salt field with increasing Delta outflow (Fig. 6). In addition, the strength and extent of modeled stratification increased as flow increased, particularly in San Pablo Bay at the highest flow (Fig. 6).

The volume of the estuary in different salinity ranges showed the interaction of salinity with bathymetry and how this interaction varied with flow (Fig. 7). The general pattern was for the entire distribution to shift toward lower salinity as flow increased. The freshwater portion of the estuary resolved by the model grew with flow as expected. The volume between salinities of 5 and 10 increased markedly because of the freshening of deep areas in Carquinez Strait and then the inundation of extensive shallow areas of San Pablo Bay (Figs. 6 and 7). The deeper more saline regions of Central and South San Francisco Bay that comprise most of the volume of the estuary became somewhat fresher but were less responsive than the fresh and brackish regions to changing flow. Nevertheless, because of their size, these regions contributed to a substantial increase in volume between salinities of 20 and 30 as flow increased, at the expense of salinities >30.

Several examples show the relationships of habitat index H to X_2 (Fig. 8; see Table 1). In most cases, the slopes had very small confidence limits (i.e., the bootstrap samples were close together). The habitat–X_2 relationships generally had zero to slightly negative slopes for species that spawn in the ocean or in the lower estuary and negative slopes for species that spawn in freshwater (Fig. 9; see Table 1 for life history information). Habitat–X_2 relationships based on catch per trawl were similar to those based on frequency of occurrence.

Slopes of the abundance–X_2 relationships were mostly inconsistent with slopes of the habitat–X_2 relationships (Fig. 9). For bay shrimp and starry flounder, the habitat indices were not related to flow, whereas abundance indices for both species were moderately related to flow. Pacific

Table 2 Summary statistics for X_2 relationships based on species and sampling programs represented in Fig. 3 (bold), the same species from other sampling programs, and other common species

Species	Source	*N*	*p*	Intercept	Slope	Step
Bay shrimp	Bay OT	26	<0.0001	3.7	−0.02±0.01	
Starry flounder	Bay OT	27	0.0006	4.7	−0.03±0.02	−0.64±0.45
Pacific herring	Bay MW	26	0.09	2.5	0±0.02	−0.49±0.44
American shad	MWT	38	0.004	4.0	−0.013±0.009	0.21±0.20
American shad	Bay MW	25	0.004	4.9	−0.018±0.012	
Delta smelt (1959–1981)	TNS	20	0.018	−0.3	0.022±0.017	
Delta smelt (1982–2007)	TNS	25	0.38	0.9	−0.007±0.016	
Delta smelt	MWT	38	0.14	2.6	0.001±0.01	−0.277±0.278
Delta smelt	Bay MW	26	0.6	3.1	−0.007±0.03	
Longfin smelt	MWT	38	<0.0001	7.0	−0.05±0.01	−0.81±0.28
Longfin smelt	Bay MW	26	0.0001	8.0	−0.06±0.03	−0.75±0.60
Longfin smelt	Bay OT	27	<0.0001	8.1	−0.06±0.02	−0.46±0.36
Sacramento splittail	MWT	38	0.0002	3.0	−0.028±0.013	
Striped bass	TNS*	32	<0.0001	4.6	−0.025±0.011	−0.79±0.30
Striped bass	TNS	44	<0.0001	2.5	−0.019±0.015	−1.18±0.31
Striped bass	MWT	38	<0.0001	4.1	−0.011±0.014	−0.90±0.31
Striped bass	Bay MW	26	0.0006	5.8	−0.027±0.020	−0.93±0.44
Striped bass	Bay OT	27	0.0001	5.2	−0.016±0.012	−0.73±0.27
Northern anchovy	Bay MW	26	0.8	3.8	−0.001±0.01	
Threadfin shad	MWT	38	0.8	3.7	−0.002±0.015	
Bay goby	Bay MW	27	0.004	4.4	0.0±0.01	0.47±0.26
English sole	Bay MW	27	0.6	4.2	0.004±0.01	
Pacific sanddab	Bay MW	27	0.0005	4.5	−0.007±0.01	0.63±0.29
Shiner surfperch	Bay MW	27	0.003	4.1	0.003±0.01	−0.46±0.24
Staghorn sculpin	Bay MW	27	0.8	4.2	−0.001±0.01	

Data sources: TNS, summer townet survey; MWT, fall midwater trawl survey; Bay MW, Bay study midwater trawl; Bay OT, Bay study otter trawl. Statistics include the total number of data points *N*, the *p* value for the fit of the model, the intercept, the slope with 95% confidence limits for X_2, and the slope with 95% confidence limits for a step function in 1987–1988. Step functions with *p* values >0.1 are not included. The fit to the delta smelt townet data required an interaction between the X_2 value and a step change in 1981–1982 (Kimmerer 2002a), so slopes are given separately for each time period. The fit to striped bass survival (indicated by an asterisk) and abundance indices had a step change in 1995–1996, and data before 1978 were excluded (see text)

herring and northern anchovy had essentially zero slopes based on abundance indices and small slopes based on habitat. The slopes for abundance–X_2 and habitat–X_2 were similar for American shad and for striped bass (Fig. 9). The strongest (negative) slope occurred in the abundance–X_2 relationship for longfin smelt, whereas the corresponding habitat relationship was weak but still negative. Habitat relationships for delta smelt and striped bass had more negative slopes in the surveys conducted in spring to early summer than in other surveys, probably because the earlier life stages occupy areas that are fresher and therefore more responsive to changing flow than the more brackish regions (Fig. 4).

Discussion

Habitat is a readily accessible concept for terrestrial and nearshore aquatic systems. Habitat loss is frequently associated with declines in abundance and diversity of terrestrial species (Kerr and Deguise 2004), and coral reef diversity is associated with the spatial extent of habitat patches (Bellwood and Hughes 2001). Arguably, the abundance of any species should be broadly proportional to the quantity of habitat of suitable quality.

Typically, two fundamental approaches are used to determine habitat suitability. First, laboratory or field observations of physiological or behavioral response to a selection of habitat variables are used to construct habitat suitability indices, which are then applied to the field. This requires a substantial investment in experimental work that grows geometrically as the number of environmental attributes increases. It is also highly unsuitable to open-water nekton because of their large individual ranges and schooling behavior. Second, field observations are made of abundance or presence of the species in samples with varying habitat attributes, and a statistical model is applied to the data. The underlying assumption that habitat availability is proportional to the observed distribution is unlikely to be met because of unobserved biotic interactions or habitat attributes not included in the model. Nevertheless, this is the

Table 3 Approximate coefficients of determination based on deviance for three alternative models each for abundance and frequency of occurrence for each species and survey

Species	Survey	Based on abundance			Based on frequency of occurrence		
		S Only (%)	*S* and depth (%)	*S* and Secchi (%)	*S* Only (%)	*S* and depth (%)	*S* and Secchi (%)
BS	Bay OT	27	29	31	25	31	30
SF	Bay OT	10	23	11	5	11	6
PH	20 mm	35	38	37	29	30	30
AS	MWT	13	13	17	3	3	7
AS	Bay MWT	37	39	43	16	17	19
DS	20 mm	20	20	35	11	12	22
DS	TNS	13	13	18	16	17	19
DS	MWT	3	4	6	2	4	3
LS	TNS	8	9	13	4	4	8
LS	MWT	10	10	25	9	9	21
LS	20 mm	21	21	32	17	18	26
LS	Bay MWT	23	25	27	19	19	23
LS	Bay OT	19	19	21	14	15	18
SB	20 mm	12	12	26	7	7	10
SB	TNS	11	15	33	7	7	18
SB	MWT	15	16	37	9	9	18
SB	Bay MWT	30	30	36	27	27	29
SB	Bay OT	29	42	30	29	34	30
NA	20 mm	40	41	41	43	43	44
NA	TNS	43	43	45	39	39	41
NA	MWT	35	35	38	43	43	44
NA	Bay MWT	22	24	24	38	39	44

Alternative models were GAMs with loess smoothers with span=0.5 and degree=2, for salinity (*S*), salinity and linear water depth, and salinity and smoothed Secchi depth. Species abbreviations as in Table 1

only approach available for open-water species, and it has been taken in this study.

Several approaches have been proposed to determine the extent of habitat based on field surveys, including the resource selection functions applied here (Manly et al. 2002). These functions describe the probability that members of a population will use a particular resource (or habitat). These functions can be based on presence vs.

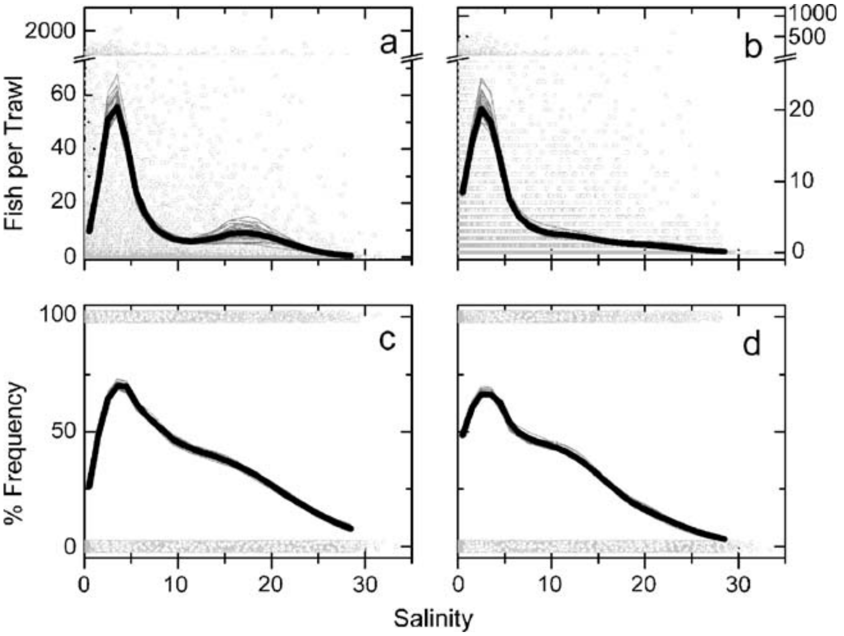
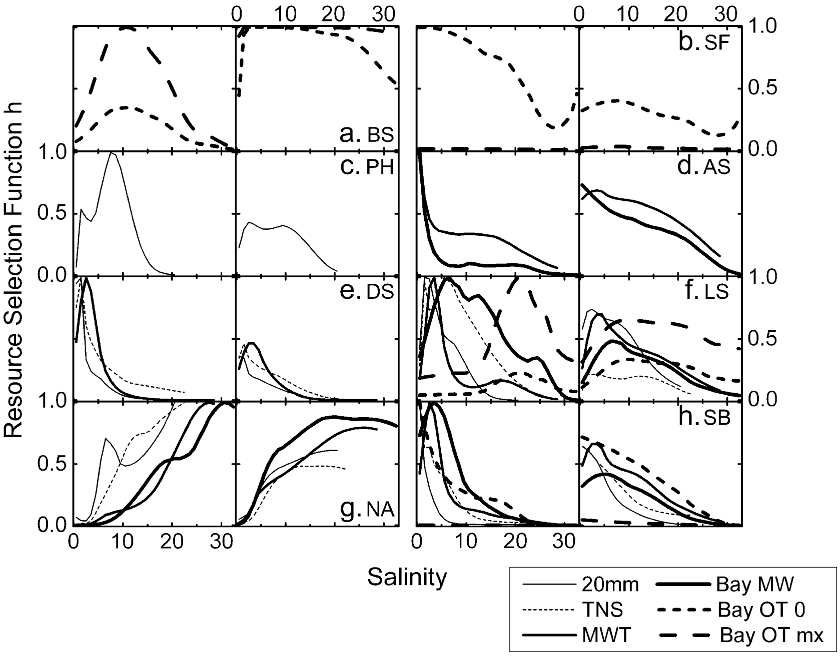


Fig. 4 Example fits of GAM curves to salinity data (*heavy lines*) with curves derived from bootstrap resampling (*thin lines*, *N*=25). Data from the fall mid-water trawl survey. **a**, **c** Longfin smelt. **b**, **d** Striped bass. **a**, **b** Abundance data (note scale changes). **c**, **d** Frequency of occurrence, with individual data points adjusted by a uniform random number for visibility

Fig. 5 Resource selection functions (**h**) for the species in Fig. 2, except that **g** is for northern anchovy instead of splittail (see text). For each species, a pair of panels displays functions based on abundance on the *left* and frequency of occurrence on the *right*. *Multiple lines* in a panel indicate data from different sampling programs (see legend). Lines for the Bay Study otter trawl are for the surface (Z_0) and bottom (Z_{max})



absence if a habitat unit can be searched completely for the species. If presence is defined by capture in the sampling scheme but absence cannot be confirmed, the dichotomy becomes presence vs. availability, provided the data are informative about the probability of observation given presence in the habitat unit (Manly et al. 2002).

For highly mobile open-water (i.e., pelagic or demersal) species, the probability of observation has more to do with the limitations of sampling gear than attributes of the habitat. Furthermore, the attributes that make up habitat quality for an open-water species can be difficult to discern. For example, a stenohaline estuarine fish becomes rarer with decreasing salinity, but it would be difficult to decide at what point the decreasing abundance would be termed “absence” even if the entire habitat could be sampled. In addition, the high abundance of some estuarine nekton populations means that some individuals are likely to be found in a wide variety of habitat characteristics (e.g., see Fig. 4a, b). Therefore, resource selection functions based on sample data require an arbitrary scaling parameter to put them into a range of (0,1), consistent with a probability (Manly et al. 2002).

Of the species we examined, only American shad and striped bass had habitat relationships to X_2 that appeared consistent with their relationships of abundance (or survival) to X_2 (Fig. 9). This provides some support for the idea that increasing quantity of habitat as defined by salinity could explain the X_2 relationships of these species, although this finding does not rule out other mechanisms.

Confidence limits for relationships of abundance with X_2 for longfin smelt, bay shrimp, and starry flounder did not overlap with those of any of the corresponding habitat

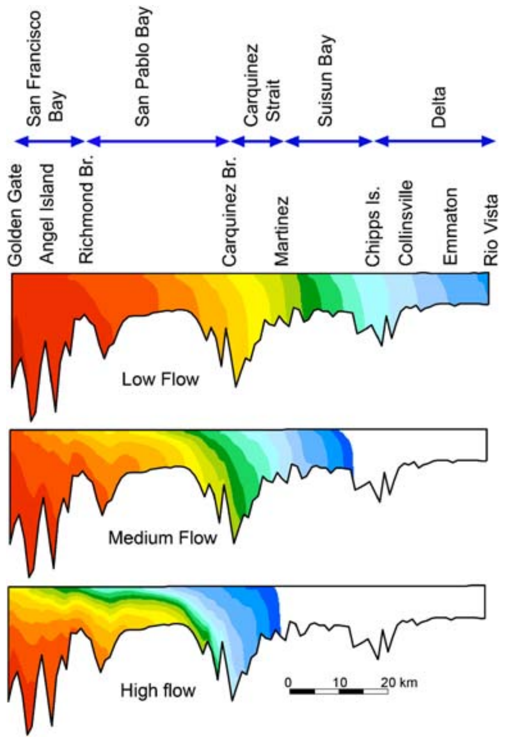


Fig. 6 TRIM3D model output. Tidally averaged salinity along the transect of the main channel from Golden Gate to Rio Vista (river kilometer 100). Locations identified by heavy lines in Fig. 1 and estuarine basins are listed at the top. Model output is given for net Delta outflows of (*top to bottom*) 110, 630, and 2810 $m^3 s^{-1}$ (lowest, middle, and highest flow)

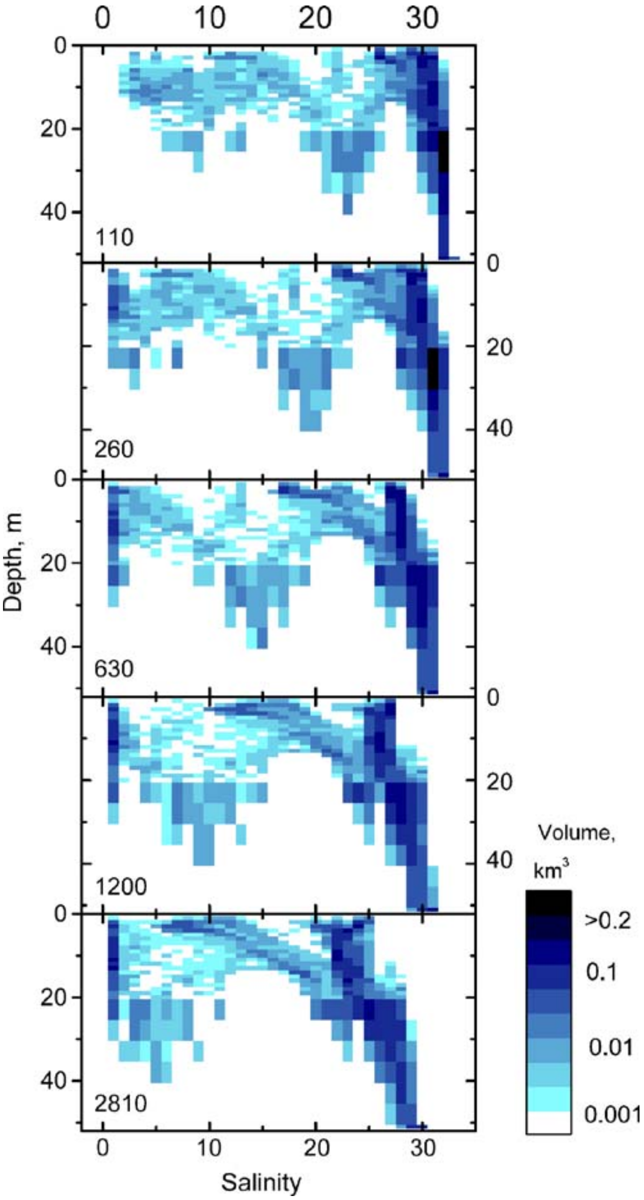


Fig. 7 Image plots of volume by depth and salinity for each of five scenarios of Delta outflow ($m^3 s^{-1}$). Salinity in increments of 1, depth in increments of 1 to 20 m, then of 5 m and truncated at 50 m (the freshwater region of the Delta not resolved by the model would increase the freshwater volume by additional 0.6 km^3)

estimates. Thus, other mechanisms are likely operating to cause these species to increase in abundance with increasing flow (Kimmerer 2002b). For bay shrimp and starry flounder, which recruit from the coastal ocean along the bottom, a plausible mechanism is related to the increase in residual circulation in the estuary with increasing flow (Monismith et al. 2002). If this increase translates to more rapid or more complete entrainment of organisms into the estuary, or more rapid transport to their rearing grounds, then presumably, survival from hatching to settlement would be higher under high-flow conditions.

Longfin smelt reproduce in freshwater and then spread rather widely throughout the northern estuary (Rosenfield and Baxter 2007). Abundance index of longfin smelt varied by about two orders of magnitude over the range of X_2 values, although abundance declined substantially in 1987–1988 and again in 2007 (lowest point in Fig. 3f). The modest slope of habitat to X_2 would allow for only about a twofold variation in abundance index over that X_2 range. Furthermore, the extent of the longfin smelt population in terms of distance up the axis of the estuary decreases with increasing flow (Fig. 10 in Kimmerer 2002b). Therefore, although increases in quantity of habitat may contribute, the mechanism chiefly responsible for the X_2 relationship for longfin smelt remains unknown. It may be related to the shift by young fish toward greater depth at higher salinity (Fig. 5f), possibly implying a retention mechanism.

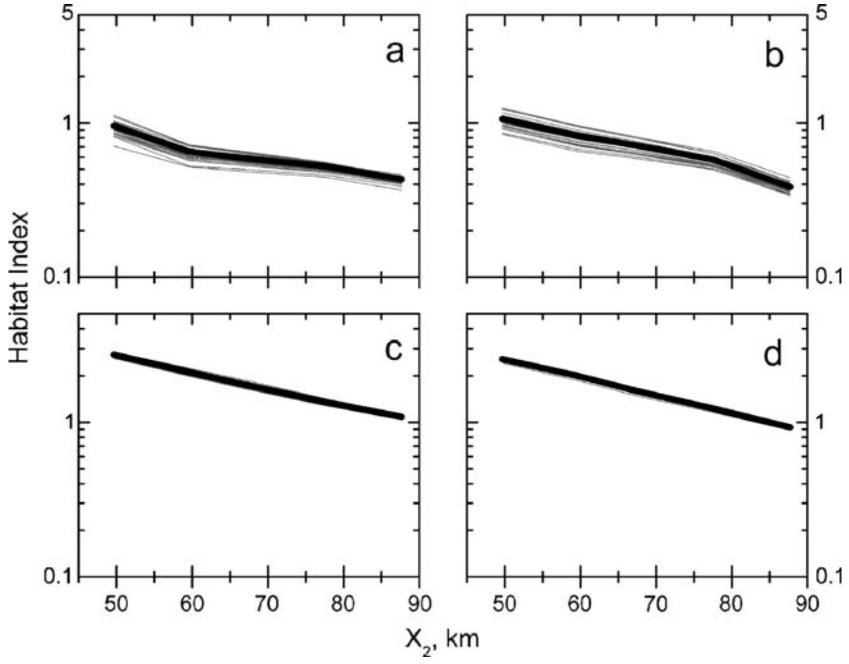
Habitat for northern anchovy was negatively related to X_2 using data from the fall midwater trawl, but unrelated using data from the Bay Study midwater trawl. Since the two surveys use the same gear, the difference is likely due to the differences in spatial coverage; the fall midwater trawl survey can miss the high-salinity regions where northern anchovy is most abundant (Kimmerer 2006). The Bay Study data are therefore more applicable to northern anchovy than data from the fall midwater trawl, and they gave a zero slope for habitat vs. X_2, consistent with the abundance index.

Habitat indices for Pacific herring were at most weakly related to flow, but the abundance index was unrelated to flow (Fig. 9). Although previous reports showed a weak relationship of egg-young survival of Pacific herring to flow (Kimmerer 2002a), additional data collected between 1999 and 2007 do not support that relationship.

Habitat indices for delta smelt and striped bass not only responded similarly to flow, but the habitat selection functions for each sampling program were similar between the two species (Fig. 5). Their life histories are very different (Table 1 and references), and in particular, the long life span and time to maturity of striped bass ensure a substantial stock-recruit effect (Kimmerer et al. 2000). Survival from egg to young-of-the-year and most of the abundance indices for striped bass had significant X_2 relationships, although density-dependent survival after the first summer damps out the effects of flow on subsequent recruitment (Kimmerer et al. 2000).

In contrast, abundance of delta smelt did not vary with X_2. Most delta smelt live 1 year, resulting in less autocorrelation due to stock size than is the case for striped bass. Adding the previous year's fall midwater trawl index as a covariate did not improve the fit of the X_2 model for the fall index of delta smelt abundance. Despite the evident increase in the amount of habitat, delta smelt abundance appears to be regulated by other factors so far unidentified,

Fig. 8 Examples of habitat indices calculated from bootstrap resampling. Data from the fall midwater trawl survey. **a**, **c** Longfin smelt. **b**, **d** Striped bass. **a**, **b** Based on abundance data. **c**, **d** Based on frequency of occurrence

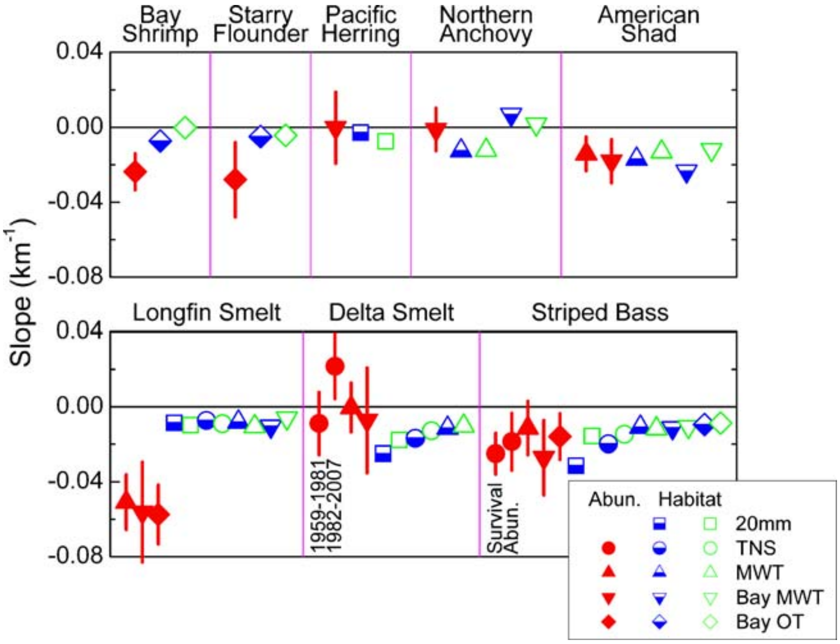


or it may be at a low enough abundance to preclude density dependence, which may be necessary for abundance to track habitat quantity.

Additional attributes of habitat loosely described as habitat "quality" might have added explanatory power to our analysis. Turbidity is an important habitat descriptor for some species and life stages (Feyrer et al. 2007; Nobriga et al. 2008). Turbidity in the San Francisco Estuary is principally due to suspended sediment concentration, which is highly variable and ultimately due to riverine inputs during floods, but responds only weakly to freshwater flow on seasonal timescales (Schoellhamer 2002). Turbidity was not included in this analysis because preliminary statistical analyses showed only a weak response of the log of Secchi depth to freshwater flow and because we had no suitable predictive model of turbidity.

Other variables such as temperature, tidal velocities, or proximity to certain bathymetric features are likely to be important attributes of habitat for some species, but these are unlikely to vary strongly with flow. In particular, temperature does not vary strongly with flow nor is it highly spatially variable (Kimmerer 2004). Thus, at least within the limitations of this analysis, the physical quantity of habitat is likely related to the observed relationships of

Fig. 9 Comparison of slopes of abundance–X_2 relationships (filled symbols, slopes and 95% confidence intervals from Fig. 2 and Table 2) with slopes of habitat–X_2 relationships determined by Eq. 1 based on catch per trawl (*half-filled symbols*) or frequency of occurrence (*open symbols*). *Shapes of symbols* indicate sampling programs (see text). Confidence limits for slopes of habitat vs. X_2 are contained *within the symbols*. The value for the X_2 relationship for delta smelt based on the townet survey (*TNS*) includes symbols for two time periods (see Fig. 2). That for striped bass includes separate symbols for survival and abundance index



only a few of the estuarine-dependent nekton species to freshwater flow. A more important drawback to our analysis might be the use of depth-averaged salinity to describe habitat, whereas the estuary is clearly stratified at some times and places. However, when we repeated some of the analyses with bottom salinity, there was no notable change in pattern. Thus, while our description of habitat is clearly simplistic, the strong spatial response of salinity to flow ensures that our model captures most of the flow-related variability.

Conditions in the coastal ocean directly affect conditions in the estuary through, e.g., effects on tide (Ryan and Noble 2007), temperature and salinity (Cayan and Peterson 1993), and species composition of flora and fauna (Cloern and Cheng 1981; Cloern et al. 2007), as well as indirectly through freshwater flow (Cayan and Peterson 1993). These effects also influence habitat for estuarine species and can strongly influence habitat use, adding variability to the habitat–abundance relationships. Some of the species discussed in detail here are widespread along the coast (northern anchovy, Pacific herring), and others are found in other estuaries (bay shrimp, starry flounder, striped bass, longfin smelt). Five other species lacking X_2 relationships are also widespread along the coast (Table 2). All of these species are likely under the influence of ocean conditions, potentially confounding relationships with estuarine conditions. However, at least for northern anchovy, abundance patterns within the estuary were unrelated to those in the coastal ocean (Kimmerer 2006).

Despite several shortcomings of this analysis, the use of resource selection functions gives a measure of habitat use that can provide insights into the distribution and abundance patterns of estuarine species. With a large sample size (Table 1), the confidence limits on the resource selection functions become tight enough to allow inferences to be made about variation in habitat and even about differences among results from different sampling programs. The results of these analyses suggest that the variation in extent of physical habitat with flow in the San Francisco Estuary could explain abundance patterns for only two species. A subsequent paper will use a modeling approach to examine how movement and retention in the estuary vary with flow and how that might underlie some of the flow–abundance relationships.

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