Research Plan to Determine the Mechanisms Underlying the "Fish-X$_2$" Relationships

Wim Kimmerer[1] and Bill Bennett[2]

1 San Francisco State University
Romberg Tiburon Center
3152 Paradise Drive
Tiburon CA 94920
415 338-3515
kimmerer@sfsu.edu

2 Bodega Marine Laboratory
University of California at Davis
P.O.Box 247
Bodega Bay, CA 94923

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Abstract

This report presents a work plan for determining the mechanisms underlying the "fish-X_2" relationships, i.e., the relationships between freshwater flow into the San Francisco Estuary and abundance or survival of estuarine fish and invertebrate species. These relationships provide part of the basis for an estuarine salinity standard. Although the relationships have changed since they were first described, they remain useful measures of the status of the estuarine ecosystem. The motivation to determine the underlying mechanisms was to learn whether the standard could be refined or made more efficient.

The principal thrust of this report is to outline the current status of knowledge about the likely mechanisms and provide a guide to determining which mechanisms are most important for which species. First we examine the relationship between freshwater flow and the physical responses of the estuary. We then update the fish-X_2 relationships and determine the relationships for additional species, and additional sampling programs, not previously examined. We then address potential mechanisms, which fall into four classes identified by letters: F, mechanisms involving a flow-related increase in food supply resulting in higher growth and survival of estuarine species; T, mechanisms involving the rate of transport by net flow patterns, resulting in reduced exposure to predation or more efficient retention; Q, mechanisms related to water quality including salinity and turbidity; and H, mechanisms depending on the variation of the quantity of physical habitat with flow that result in population responses. Several of these mechanisms are particularly promising for some species; for example, the response of splittail to freshwater flow is almost certainly due to changes in the quantity of habitat for this species (class H). Habitat quantity is examined for other species in a separate paper included as Appendix B. Transport mechanisms may be particularly relevant because of the strong responses of physical circulation to freshwater flow. Turbidity is an important environmental attribute, but a model study intended to determine its potential importance in predator-prey interactions was inconclusive.

The plan for elucidating mechanisms is presented in broad outline, leaving details to be filled in by researchers proposing to investigate the mechanisms. The plan is organized around several key principles. In particular, mechanisms must be judged using weight of evidence rather than formal hypothesis-testing, and the program should be adaptive rather than comprehensive to take advantage of learning and of the talent and knowledge of individual investigators. Several classes of studies are identified as particularly helpful, including: studies of early life stages; studies of retention and predator-prey relationships; studies of small-scale distributions of organisms; studies of growth rate using otoliths; feeding studies; and investigations of population dynamics. Many of these classes of studies should incorporate simulation models to maximize the knowledge gained from fieldwork.

Introduction

Abundance or survival of several estuarine fish and shrimp populations in the San Francisco Estuary is positively related to freshwater flow (Jassby et al. 1995). These relationships have been described in terms of "X_2", the distance up the axis of the estuary to the 2 psu (practical salinity units) isohaline. The "fish-X_2" relationships form the basis for management of the estuary using a salinity standard (Kimmerer and Schubel 1994).

The salinity standard is an ecosystem management tool in that it appears to benefit a variety of estuarine species. In spite of the recent changes in the estuary, the standard remains useful for management at the ecosystem level, but it is not a well-honed tool. Meeting the standard comes at a high cost in water (Kimmerer 2002b), leading to concerns about cost-effectiveness of the standard within the water-user community. Furthermore, some of the fish-X_2 relationships on which the standard is based have considerable statistical uncertainty, so the realized benefits of the salinity standard are not clear. Some of the relationships have changed during the period of record. Finally, the current relationships are statistical rather than mechanistic, and provide no information about how biological populations might respond under alternative configurations of the system, e.g., if an alternative water conveyance scheme is implemented, or if the physical geography of the Delta changes through choice or chance (Mount and Twiss 2005). Thus, there is a great deal of interest in improving and refining the standard. To do this will require a better understanding of the mechanisms underlying the fish-X_2 relationships.

Although progress has been made toward understanding a few of the mechanisms underlying the fish-X_2 relationships, a comprehensive research plan has not yet been developed for systematically evaluating the mechanisms. Implementing such a plan could markedly increase the efficiency with which knowledge is obtained and translated into policy.

In this report we develop a plan for determining the mechanisms underlying the fish-X_2 relationships. This plan is based on a considerable background of information on the influence of flow on the estuary, the response of various biota to flow, changes in those responses, and other factors influencing estuarine populations. Some of this information is published but much of it is still work in progress. We therefore present below a set of linked conceptual models with a thorough exploration of these topics as a basis for the research plan.

Since this project was originally proposed, substantial changes have occurred that influence how this research plan should be developed. The recent pelagic organism decline (POD, Sommer et al. 2007) involved three of the species formerly considered in the X_2 relationships, and the lower abundance since 2001 has prompted a re-evaluation of their X_2 relationships, shown below. More importantly, this change has resulted in substantial new research and monitoring, and an intense focus on the Delta and on the POD species. The resulting crisis atmosphere has reduced interest in exploring the X_2 relationships, but has also provided for some useful interactions and cross-fertilization between the POD management team and this effort.

New knowledge developed during the last few years has also narrowed the focus of the research plan. As discussed below, particle-tracking studies have provided information useful in determining whether some mechanisms are likely to be important. Analyses of export effects on

some populations have clarified some of the potential mechanisms. And advances in three-dimensional modeling of the estuary (mainly as part of this project) have revealed some important aspects of the fish- X_2 relationships.

We assume that readers of this report will be familiar with basic information on the San Francisco Estuary (Figure 1). A substantial literature on the estuary has been synthesized in several recent papers (Moyle 2002, Brown 2003, Kimmerer 2004), while others have provided thorough accounts of the status of individual species (Bennett 2005, Moyle et al. 2004, Williams 2006).

The Fish- X_2 Relationships

X_2 was developed as an indicator of the physical response of the estuarine ecosystem to changes in freshwater flow. The log of abundance or survival of various estuarine species of fish and invertebrates is negatively correlated with X_2, i.e., positively with outflow (Jassby et al. 1995). These relationships use values of X_2 averaged over several months, usually in the spring, when each fish or invertebrate species is believed to be most sensitive to flow conditions in the estuary.

In general the relationships appear to be linear in X_2, and for some species a change in intercept has occurred at some time, and for one species a change in slope has occurred (Figure 2). A linear relationship of log abundance or survival with X_2 means that the predicted response variables change by a constant fraction for each kilometer change in the mean X_2. This does not mean that the underlying mechanisms themselves are linear; actually some relationships are likely to be nonlinear or step changes. However, the temporal averaging of X_2, tidal action within the estuary, and other influences on abundance or survival will all smooth or obscure step changes or other nonlinear responses. A straight line is the simplest model to fit, and with the number of data points available no alternative can be detected (e.g., by inspection of the residuals or using a nonlinear term in the statistical models).

The lack of a significant relationship of abundance to X_2 means either that there is no relationship or that it is weak and obscured by other sources of variability. These alternatives cannot be distinguished statistically. In some cases no response, or an inverse response, of abundance to X_2 can be inferred from the life history and habitat of the species. For example, marine species generally have no relationship or an inverse one (i.e., positive slope with X_2, see below) presumably because they leave the estuary when it becomes too fresh.

Flow and X_2

Although there has been some argument about whether flow or X_2 is more suitable as the independent variable in these relationships, it hardly matters statistically since the long averaging period means that flow and X_2 are very closely correlated. Although flow is clearly the ultimate cause of variability in salinity patterns, X_2 has several advantages as an independent variable. For one thing, it provides a geographic frame of reference that is more intuitive than a flow variable. Second, X_2 can be determined by interpolation between continuous monitoring sites, whereas delta outflow has only recently been measured, so the data record is short. Third, most

estuarine species cannot be affected directly by flow unless it is extremely high, because of complete vertical mixing that usually occurs at low salinity in shallow water (Burau 1998); thus, X_2 more accurately reflects the conditions to which most estuarine species are exposed.

The choice of the 2 psu isohaline was not arbitrary. This salinity is high enough to be unambiguously derived from the ocean, as opposed to agricultural drainage. X_2 marks the approximate landward limit of estuarine stratification and circulation, and therefore the transition between the tidal freshwater and brackish parts of the estuary. For that reason, seaward of this point vertical variability in circulation becomes important, and 2-dimensional modeling is inadequate to capture estuarine dynamics. In addition, it is the approximate center of the "low-salinity zone" or LSZ, habitat for certain estuarine-dependent species, including several zooplankton species (Kimmerer and Orsi 1996, Kimmerer et al. 2002a, b) and young striped bass (Kimmerer et al. 2001).

Daily freshwater flow into the San Francisco Estuary has varied over ~100-fold in the past three decades. Numerous processes in the estuary change with changing river flow; for discussion we consider here an increase in river flow (Table 1). Stage increases, resulting in more inundation of marginal and isolated floodplains. Velocity also increases, resulting in more rapid transport of materials and organisms down the rivers. The combination of higher stage and velocity with overland runoff increases scouring and sediment resuspension so that sediment concentrations increase with river flow. Concentrations of other dissolved and particulate constituents (e.g., nutrients, organic matter) may increase or decrease with increased flow. A constant loading of a constituent to the estuary would arise with a constant input to the rivers such as from a sewage treatment plant, so that concentration in the riverine input would vary inversely with flow. Otherwise the loading or total flux to the estuary of various substances and organisms must generally increase with increasing flow (Kimmerer 2002b). Some contaminants may increase in concentration during a "first flush" event and then decrease, but total loading is still higher when flow is high (e.g., contaminants, Bergamaschi et al. 2001).

Residence time for water is inversely related to river flow throughout the estuary (Walters et al. 1985). Residence time for conservative tracers should behave similarly, whereas the retention of particles depends on the interaction of particle settling and three-dimensional circulation, discussed below. Retention of organisms is still more complex, and an important theme for this research plan as discussed below. Net flow through the northern estuary at any cross-section, averaged over a spring-neap tidal cycle, is equal to total river flow into the estuary upstream of that cross-section. Since most of the flow through the estuary comes through the Delta, net flow is therefore closely related to Delta outflow.

The barotropic (i.e., water level) pressure gradient between the river and the ocean tends to push seawater out of the estuary. This is opposed by the baroclinic gradient (i.e., the density gradient due mainly to salinity), and by tidal mixing (predominantly tidal pumping and trapping), both of which tend to move salt water into the estuary. The interplay among these forces is complex and depends on the bathymetry of the estuary (Monismith et al. 2002), but the net result of an increase in freshwater flow is a corresponding seaward movement of X_2. Daily X_2 has been modeled as a function of the log of Delta outflow and the previous day's X_2 value such that the response time of the estuary to changes in freshwater flow is on the order of 2 weeks (Jassby et

al. 1995). Alternatively, the flow- X_2 relationship has been represented on theoretical grounds as a power function (Monismith et al. 2002), which when reduced to steady state becomes:

$$X_2 = 167Q^{-0.14} \tag{1}$$

where Q is daily net Delta outflow ($m^3 s^{-1}$).

When the salt field shifts seaward, salinity at any point changes. This can have important effects on benthic or salt marsh organisms, whereas pelagic organisms move with the water. In addition, the location of any salinity value changes, and the area or volume bounded by a given salinity range can change. To the extent that habitat for species is defined by salinity, the quantity of habitat in a given salinity range may increase or decrease. The freshwater volume of the estuary must increase, and therefore the brackish to saline volume must decrease. However, the details of these changes are complicated by the interaction between three-dimensional flow patterns and the complex bathymetry of the estuary. The end result is that the area or volume bounded by low to moderate salinity increases, while the region in high salinity decreases (Kimmerer et al. in prep.).

Salinity stratification results from an interaction of baroclinic and barotropic forcing, tidal flows, and bathymetry, sometimes influenced by wind. Generally stratification is highest with a strong baroclinic gradient and weak (neap) tides in a deep channel. As flow increases the baroclinic gradient increases and the landward limit of the salinity field is moved from the shallow expanses of Suisun Bay into deeper areas in Carquinez Strait and San Pablo Bay. This combination enhances stratification and can shift the system from a state of tidally periodic stratification to persistent stratification over several days (Monismith et al. 1996). Where the estuary is stratified, the baroclinic gradient causes gravitational circulation, whereby the tidally averaged flow near the bottom is landward, and that at the surface is seaward.

The exponent –0.14 in Equation 1 is smaller in magnitude than expected theoretically, probably because the salinity field is compressed with increasing flow, resulting in increased stratification especially in deeper waters in seaward reaches of the estuary, and increased landward salt flux due to gravitational circulation (Monismith et al. 2002). In addition, exchange through the Golden Gate, largely due to tidal pumping, is enhanced by increased freshwater flow into the estuary (Fram et al. 2007). The "stiffness" of the estuary, whereby X_2 moves less than would be expected for a given change in flow, also implies that these forms of residual circulation are very sensitive to changes in the length of the salinity gradient. Because organisms that stay near the bottom can become entrained in the landward-flowing bottom layer, gravitational circulation may play a key role in retention of organisms and therefore in one class of mechanisms for the X_2 relationships; however, lateral flow patterns are also likely to be important.

Statistical analysis of the fish- X_2 relationships provides little help in determining the underlying mechanisms. The fundamental problem with statistical analysis is the close relationship among freshwater flow, X_2, and a host of other variables (Table 1). Examples include the proportion of flow diverted onto floodplains, the proportion exported from the Delta, and the loading into the estuary of various substances and organisms (Kimmerer 2002b Figs. 6-7). Net Delta outflow is equal to inflow minus net diversions in the Delta, but the overwhelming influence of very high

winter flows make the correlation between inflow and outflow very strong (r=0.99 for daily values from 1955-2006, data from http://www.iep.ca.gov/dayflow/). The correlations among different flow-related variables preclude statistical resolution of the mechanisms but, together with consideration of species' life histories, may offer insights into how these mechanisms may work. For example, Sacramento splittail spawn on floodplains such as the Yolo Bypass (Sommer et al. 1997), and floodplains are inundated by high river flows. Inundation increases spawning or rearing habitat for splittail, which results in higher production and juvenile abundance during high-flow years (Sommer et al. 1997; Moyle et al. 2004; Feyrer et al. 2006).

Updates to the Fish- X_2 Relationships

The original report on the fish- X_2 relationships included 10 response variables measured through 1990 or 1991: supply of organic carbon, abundance of mollusks, mysids, and the copepod *Eurytemora affinis*, abundance indices for the bay shrimp *Crangon franciscorum*, delta smelt, longfin smelt, striped bass, and starry flounder, and a survival index for striped bass from egg to young-of-the-year (Jassby et al. 1995). These relationships were re-examined in light of changes in the estuarine foodweb following introduction of the overbite clam *Corbula amurensis* in 1986 (Kimmerer 2002a). Three additional species were included in the analysis: abundance indices of American shad and Sacramento splittail, and a survival index of Pacific herring from egg to young-of-the-year. Abundance indices were taken from the most suitable source for each species: the San Francisco Bay study for the more marine species, and the fall midwater trawl for most other species. Delta smelt and striped bass abundance indices were originally analyzed based on the fall midwater trawl (Jassby et al. 1995) but in the 2002 analysis data from the summer townet survey were used, and a striped bass survival index was calculated from its abundance index.

X_2 values used in analyses were either monthly means for lower trophic levels, or were averaged over time periods that specialists from the Department of Fish and Game considered important for each species, generally the period when larvae are present in the system (Jassby et al. 1995). The later analysis included a step change in 1987-1988, except for the delta smelt summer townet index, which clearly changed in 1981-1982. In each case the step change was entered either as an interaction with X_2 (in which case each time period was analyzed separately) or as a change in intercept.

Here we update the X_2 relationships through 2005-2007 (depending on the availability of data) for the fish and shrimp species previously examined. We also present X_2 relationships for the same species from alternative sampling programs, and for other species not previously considered. Except for starry flounder (see Jassby et al. 1995) the focus is on young-of-the-year when they have been distinguished in the reported indices. For the species previously examined, the same X_2 averaging period was used. For other species the averaging periods were either those selected by specialists as in Jassby et al. (1995), or March-June of each year. The annual value of X_2 averaged over March-June was correlated with monthly values from February and July through September at r = 0.76 to 0.86, so the exact choice of months makes little difference to the results.

Analyses of relationships to X_2 followed previous approaches (Kimmerer 2002a). For most species log of abundance was related to X_2 averaged over several spring months when each species is likely to be most vulnerable to freshwater flow effects. In contrast to previous analyses we used abundance rather than survival for Pacific herring. For each species we included a step change in 1987-1988 to allow for the possibility of an effect of declining food supply. For delta smelt in the townet survey the slope changed in 1981-1982 so that step was included in the model as an interaction term.

For striped bass two kinds of response variable were used, and the step was in 1995-1996 (we do not know the reason for that timing). Abundance indices from each of the sampling programs were truncated to data after 1977 (summer and fall surveys only) because the large decline in egg production in 1976-1977 caused a substantial decline in YOY (Kimmerer et al. 2000). We also used survival from egg to the first summer, calculated as described in Kimmerer (2002) with one modification. Briefly, egg production was calculated from adult abundance by age determined as Petersen estimates from mark-recapture studies, and from age-specific fecundity (Kimmerer et al. 2000). The summer abundance index was the mean catch per trawl in the summer townet survey, which is closely related to the townet index used previously (r=0.95 between annual values for the entire time series). Adult striped bass were sampled only during even years between 1994 and 2002, and abundance estimates are not yet available for 2006-2007. We filled in these values by interpolation (level extrapolation for the last 2 years) for graphs only, but excluded the resulting values from statistical analysis.

For the Bay Study species not previously examined we first calculated a regression of log of abundance index on X_2, then used a regression tree with a single branch to determine the best timing of any step change in the residuals. This timing was then used in a linear model with X_2 and the step change, entered without an interaction term, as:

$$Y = \alpha X_2 + \beta \text{YearCat} + \varepsilon \qquad (2)$$

Most of the species commonly collected in the Bay Study are euryhaline marine species for which strong responses to freshwater flow or its correlates would not be expected. Nevertheless, these species can provide a useful contrast to those species that do respond positively to outflow.

The X_2 relationships (Figure 2, Table 2) are not markedly different from those previously published, except that the slope of the X_2 relationships of abundance index of Pacific herring was essentially zero. The slope of egg-YOY survival, calculated as in Kimmerer (2002), had no significant relationship to X_2. Species for which data were available from more than one survey showed consistent patterns in all of the surveys, except for delta smelt: smelt captured in the summer townet survey had a change in slope after 1981 (Figure 2) whereas smelt captured in the midwater trawl survey had a step change in 1987-1988 and essentially zero slope with X_2.

The POD years 2002-2007 were marked by lower abundance than expected for delta smelt, longfin smelt, striped bass, and also splittail, not considered a POD species (Figure 2). Longfin smelt recovered to its post-clam abundance in 2006, but had its lowest index in 2007, suggesting a possible further step change in its X_2 relationship. The delta smelt midwater trawl index (not shown) also was substantially depressed after 2001. Data from the Bay Study revealed different

patterns. Delta smelt was exceptionally low in 2001, 2002, and 2006 but not the intervening years. Striped bass collected from both the midwater and otter trawls had depressed values in 2002-2004, but recovered after that to the post-clam levels. Sacramento splittail showed no long-term change. Longfin smelt indices from the Bay Study midwater trawl were highly variable and low during 1991-1992 and after 2001, whereas in the otter trawl their abundance index was not lower during the POD years than the rest of the post-clam period.

A few of the other common species not included in the previous analyses had significant X_2 relationships (Table 3). Notably, abundance index of yellowfin goby was negatively related to X_2, whereas those for jacksmelt, barred surfperch, the shrimp *Heptacarpus* species, and the crab *Cancer antennarius* were all positively related to X_2. Threadfin shad was negatively related to X_2 in the Bay study but not the fall midwater trawl. Most of the species had significant step changes but in various years (Table 3), and about equally divided between positive and negative changes. Ten of the Bay Study indices had significant step changes during 1986-1989, which may be linked to the changes in the ecosystem when *C. amurensis* became abundant. The probability of this many or more step changes during a 3-year period is <0.007, compared to the alternative of step changes distributed randomly between 1984 and 2001. Thus, it is likely that at least some of these changes were due to the declines in productivity of lower trophic levels (Kimmerer 2002a, b). Of the species that changed during 1986-1988, the ones that declined in abundance were planktivores, while those that increased were generally demersal.

Overall, species that require low to brackish salinity for rearing more often had negative relationships to X_2, meaning positive relationships to flow. Some of these species, notably striped bass but also splittail, delta smelt, and longfin smelt, may have gone through a further decline after 2001. A few marine species have negative relationships to flow, presumably because they are stenohaline and leave the estuary when salinity declines.

These contrasts are useful in elucidating mechanisms. For example, the species that rear in fresh to brackish water have negative X_2 relationships whether they spawn upstream or downstream of the LSZ. This implies that something about this specific habitat is involved in the mechanisms. Still, the attributes of this habitat do not apply to all species found there, because delta smelt do not respond similarly to longfin smelt, for example. Thus, X_2 mechanisms likely involve interactions between characteristics of habitat and those of the species.

Potential mechanisms

Our focus is on estuarine-dependent species of higher trophic levels, namely fish and the bay shrimp *Crangon franciscorum*. The mechanisms most likely differ among these species because of their varied life histories and seasonal patterns of recruitment. Furthermore, some species may be affected by flow or X_2 through more than one mechanism (Bennett and Moyle 1996).

Figure 3 examines the life stages and locations that are most likely involved in the X_2 relationships for each of the species in Figure 2. Table 4 and Figure 4 summarize some of the more plausible mechanisms that have been identified and are explored below. Logic flow diagrams for selected species with significant X_2 relationships and multiple potential

mechanisms (Figures 5-7) provide a guide to the steps needed to investigate each of the more promising mechanisms.

We do not claim to have covered all of the mechanisms that could be operating, and our choices of the most promising ones may be incorrect. A certain amount of judgment is required in selecting which mechanisms to focus on. Here we have focused on those that have the most support in data and analyses. However, surprises always occur in research, and if this research plan is pursued the direction will no doubt change.

We make several key assumptions in conducting this analysis:
- Each species/life stage occupies a range of conditions loosely described as "habitat quality," including at least temperature, salinity, water depth, turbidity, and possibly tidal velocity. Abundance and probability of capture are higher within certain ranges of these variables.
- Analyses consider how mechanisms operate as flow changes, all else being equal; that is, variability due to other causes is considered noise for the purpose of each analysis, although statistical models of flow effects may be more powerful if other known factors are included (e.g., the temporal step changes discussed above).
- A larger extent (either area or volume depending on the species/life stage) of habitat within the range used by the species should generally result in a proportional increase in abundance if habitat is limiting to that species/life stage.
- Many aspects important in the habitat of fish are not addressed by any sampling program (e.g., habitat complexity, bathymetric features, tidal velocity)
- More than one mechanism could operate for a given species, and interactions among factors may be important to some mechanisms (many of the proposed mechanisms deal explicitly deal with interactions).

Ultimately, determining the mechanism(s) behind the X_2 relationship of each species will be based on weight of evidence. Although some mechanisms for some species can be ruled out or at least assigned a low probability of contributing, the most that can be said in support of a particular mechanism is that it is consistent with the observed X_2 relationship. For example, Kimmerer (in press) concluded that the weak and non-significant relationship between delta smelt summer index and X_2 since 1981 (Figure 2) was consistent with a mechanism by which export losses of delta smelt were higher when X_2 was landward than seaward. However, this is a weak inference in the absence of other corroborating evidence, since the confidence limits around the observed relationship are wide (including zero), and no other mechanisms have been examined. More importantly, this mechanism fails to explain the change in slope that occurred after 1981 (Figure 2).

Any mechanism must operate through its influence on one or more vital rates of the species, including mating success, reproductive rate, growth, or survival. In turn, each of these vital rates may be affected at a particular life stage, requiring a particular change in the environment at a particular location (Figure 3). For example, the success of transport to rearing habitat affects survival of larvae and early juveniles, whereas availability of spawning habitat affects reproduction (Figure 3). Likewise, since striped bass spawn in freshwater, transport affects eggs and early larvae in freshwater and the LSZ, whereas a transport mechanism applying to bay

shrimp and starry flounder would have to operate on late larvae and early juveniles between the ocean and the LSZ.   The specific vital rate affected, and the life stage and location in which this vital rate varies, can be used to narrow the range of mechanisms for each species, and to help focus the design of studies intended to assess the mechanisms.   Note that the location at which a mechanism operates may be far removed from the 2 psu isohaline itself, and the mechanism may operate at a different life stage from that used to detect the X_2 relationship. Therefore detecting an important mechanism will require consideration of how flow affects conditions in different regions and life stages.

At the same time, mechanisms to explain X_2 relationships must be linked somehow to one of the correlates of freshwater flow (Table 1). A factor that influences a species and life stage (e.g., food limitation) can constitute part of a mechanism only to the extent that it varies with flow. Of the numerous factors that affect species, only a limited subset meets this criterion. This is clearly visible in the X_2 relationships that changed in intercept but not in slope after 1987 (Figure 2): this change was almost certainly due to a decline in food supply, but the lack of change in slope suggests that the mechanisms underlying the X_2 relationships differed from those underlying the step changes.

Mechanisms that could apply to some or all species are related to four key influences on the life cycle: food supply, transport (including losses to water diversions), water quality including particularly water clarity (relating to predator avoidance), and physical habitat. Predation is not listed as a separate class of mechanisms, since there is no evidence that predator abundance decreases as freshwater flow increases. Predation could be involved indirectly as the immediate cause of mortality in several potential mechanisms, but the flow variability arises through, e.g., changes in vulnerability to predation. We discuss potential mechanisms in turn below, presenting analyses that help to focus on key aspects of each mechanism.

Each mechanism is described by a letter for the general class of mechanism, a sequence number, and in most cases a lower-case letter indicating that the mechanism has several parts, each necessary for the mechanism to operate as described.

Mechanism F: Food supply is one of the usual suspects in any analysis of variability in population size. Several proposed mechanisms lead to food limitation through several alternative causal pathways (Table 4, Figure 4). This class of mechanisms refers specifically to those arising through variation in the rate of organic matter supply to the foodweb. Several mechanisms in other classes may also operate through their effects on availability or access to food (Figure 4).

Feeding, particularly early feeding by larval fish, can be a key mechanism for variability in recruitment (Lasker 1975). Within the San Francisco Estuary, nearly every quantitative study of reproduction or feeding by invertebrates has demonstrated food limitation. Growth of cladocerans speeds up as chlorophyll increases in Delta water (Müller-Solger et al. 2002). Copepods feed (Bouley and Kimmerer 2006; Hooff and Bollens 2004) and reproduce (Kimmerer et al. 1994, Durand 2006 CALFED Science conf) more slowly when food supplies are limited. Egg production of copepods in San Pablo, Central, and South Bays increase during spring phytoplankton blooms (Kimmerer et al. 2005). The Asian clam *Corbicula fluminea* is likely

food limited most of the time (Foe and Knight 1985). Food limitation in fish has not been examined much, although Bennett et al. (1995) found no evidence of starvation in larval striped bass over a 4-year period. Juvenile delta smelt showed signs of low food consumption in at least one year (Bennett 2005), and an index of survival of delta smelt from summer to fall is correlated with zooplankton biomass (Kimmerer in press). Striped bass and longfin smelt were in poor condition in the main ship channel of Suisun Bay compared to the northern channel in 1996 (Hobbs et al. 2007). Food limitation of diving ducks in San Pablo Bay can also be inferred from their feeding patterns and the decline in abundance of clams each winter (Richman and Lovvorn 2004).

In estuaries generally, an important mechanism by which food limitation can be related to freshwater flow has been described as the "agricultural model" (Nixon et al. 1986, Nixon 1993). According to this model, increasing nutrient loading with increasing flow results in stimulation of phytoplankton production (Mechanism F1a, F1b). Phytoplankton blooms can also occur through stratification, which increases with freshwater flow in some parts of the estuary (F2a, F2b). An alternative mechanism for effects of nutrients has recently been proposed: high ammonium concentration mainly from sewage treatment plants may suppress the growth of diatoms, so dilution of ammonium by high flow could promote diatom blooms (F3a, F3b; Wilkerson et al. 2006, Dugdale et al. 2007). In either case an increase in phytoplankton production boosts production of organisms (zooplankton, amphipods, clams) that provide food for fish and shrimp (F1c, F2c, F3c).

The principal argument against mechanisms F1, F2, and F3 is that there is little evidence for a positive response of chlorophyll concentration throughout the northern estuary to freshwater flow. Phytoplankton production in the San Francisco Estuary is most commonly limited by light rather than nutrients (Arthur and Ball 1979, Cole and Cloern 1984, Cloern 1999), and nutrient concentrations in the northern estuary are generally high (Hager and Schemel 1992), suggesting that the agricultural model does not apply at least to the northern estuary. Chlorophyll in the LSZ showed little response to freshwater flow either before or after *Corbula amurensis* became abundant (Kimmerer 2002a). In the Delta in spring, chlorophyll actually decreased with increasing flow, apparently because of decreasing residence time (Jassby et al. 2002). Chlorophyll concentration on floodplains also decreased with increasing flow as residence time decreased (Sommer et al. 2004). Thus, there is no evidence that seasonally-averaged phytoplankton biomass responded positively to flow in either of these regions. Nevertheless, local or regional effects could be important, and intermediate levels of connectivity between habitats may maximize production (Cloern 2007). Stratification and therefore the productivity of ephemeral spring blooms in South San Francisco Bay respond positively to high freshwater outflow from the Delta (Cloern 1991).

Exogenous organic carbon may provide important energy supplies to estuaries (e.g., Smith and 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 (Canuel et al. 1995, Jassby and Cloern 2000, Sobczak et al. 2005, Sobczak et al. 2002). Although biomass in the Delta decreased with increasing flow in spring, loading to the LSZ still increased (Jassby et al. 1993, 2002). With an increase in the supply rate of bioavailable

carbon with flow, bacterial production could increase with flow (F4a, F4b). There is no information on the response of bacterial production to flow, although bacterial abundance probably declined following the spread of *C. amurensis*, which is capable of filtering bacteria from the water column (Werner and Hollibaugh 1993, Hollibaugh and Wong 1996).

The stimulation of bacterial or phytoplankton production due to increased carbon loading could support higher trophic levels only if there were equivalent levels of response to flow in the intermediate trophic steps, i.e, zooplankton and particularly rotifers (F1c-F4c; see Holst et al. 1998), but this was not observed. Abundance of consumer organisms responded strongly to the step change in 1987-1988, and responses to X_2 were weak or nonexistent, or they changed slope in 1987-1988 (Figure 6 in Kimmerer 2002a).

It could be argued that production of food organisms and phytoplankton could increase even without an increase in biomass. However, the evidence does not support this. First, specific growth rate (i.e., per unit biomass) of phytoplankton is related to available light and turbidity (Cole and Cloern 1984, Jassby et al. 2002), and turbidity increases somewhat as flow increases (see below). Jassby et al. (2002) argued that primary production in the Delta followed trends in chlorophyll concentration, and the same argument holds for Suisun and San Pablo Bays. Specific growth rate of zooplankton is controlled by temperature (McLaren 1978) and food concentration (Vidal 1980, Kimmerer and McKinnon 1987), which are unresponsive to X_2 if food supply is related to phytoplankton biomass. Reproductive rate of the copepod *Eurytemora affinis* did not vary with flow or chlorophyll (Kimmerer et al. 1994). Similarly, no changes with flow were detected in fecundity of *Neomysis mercedis* (Orsi and 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.

This is not to say that variation in primary production or organic carbon supply has no effect. Food limitation is very likely the cause of the declines in several of the X_2 relationships in Figure 2, except possibly for delta smelt. These declines coincided with the massive changes in the foodweb following the introduction of *Corbula amurensis*, which among other things resulted in a 10-fold decline in mysids, a principal food for striped bass and longfin smelt (Orsi and Mecum 1996, Kimmerer 2002a, 2006). Thus it appears that the 1987-1988 decline in phytoplankton propagated up through rotifers, copepods, and mysids, and into starry flounder, longfin smelt, striped bass, and northern anchovy (Figure 2; Kimmerer 2002a, b, 2006). However, these foodweb effects are statistically independent of the respective X_2 relationships of fish and shrimp. Thus, these shifts actually argue that the slopes with X_2 are probably not caused by any aspect of food limitation, but rather due to changes in physical habitat (Kimmerer 2002a).

Despite the above arguments it is still possible that food supply for some species increases with increasing flow, at least within some range of flow. The flux of organic matter into the estuary must increase with flow (Jassby et al. 1995), and may support the microbial foodweb. Unfortunately microbial activity (e.g., bacteria, ciliates) has not been estimated for more than a few brief periods. This production is unavailable to most fish directly. Without an increase in zooplankton biomass with flow, there seems to be no way for this mechanism to result in flow-related variability of growth of planktivorous fish. However, we cannot be certain at this point

that our measurements are inconsistent with this mechanism, especially because feeding occurs at much smaller scales than are measured during field studies. Furthermore, fish that can feed on benthic or terrestrial prey may see an increase in food supply without any effect on zooplankton. This mechanism is too important in other estuaries, and such an obvious candidate for important ecological effects, to be ruled out so early.

Mechanism T: Transport refers to movement of organisms, how that may be affected by conditions related to flow, and how it might in turn affect one or more vital rates. Transport includes movement away from hazards such as water diversions in the Delta, movement toward habitats for spawning or rearing, and local movement that may alter habitat characteristics.

The principal diversions are the south Delta water export facilities and the numerous in-Delta agricultural diversions (Herren and Kawasaki 2001), but this category should also include diversions into the North Bay Aqueduct, Montezuma Slough when salinity control gates are operating, the Contra Costa Canal, and power plant cooling intakes. These all operate differently and have different effects, but in terms of potential X_2 mechanisms they are similar in representing fixed sites of mortality risk. For species and life stages that move through the Delta (e.g., striped bass eggs and larvae) higher flow rate may reduce the time of exposure to export pumping, thereby resulting in higher survival with higher flow. This has been demonstrated with particle tracking models (T1, Kimmerer and Nobriga 2008). Furthermore, the covariability of adult returns of San Joaquin Chinook salmon with freshwater flow 3 years earlier (Speed 1993) could be due to this mechanism, although it could also be due to conditions in the rivers. Flooding of the Yolo Bypass in high-flow periods provides an alternative pathway for movement of young salmon (Sommer et al. 2001), potentially reducing the probability of entrainment in Delta diversions.

Alternatively, populations of organisms that use low salinity as habitat will be further from these hazards when X_2 is further seaward (T2, Kimmerer in press). Foodweb organisms may also be vulnerable to export pumping and other diversions (TF3a), particularly those that reside entirely or mostly in freshwater.

Several mechanisms (T4-T6) involve the movement of organisms from one habitat to another. For these mechanisms to underlie an X_2 relationship requires both that the population-weighted rate of movement increases with increasing flow (T4a-T6a) , and that growth or survival is higher for organisms that get to the new habitat more quickly (T4b-T6b). Thus, there may be some hazard during the migration, or the energy expenditure for migration may reduce survival.

Many aquatic organisms migrate from one habitat to another using various cues, possibly including freshwater flow or its covariates (T4a). Freshwater flow is likely an important cue for migration in the rivers and floodplains (Harrell and Sommer 2003), if not the estuary proper. Diadromous species such as Chinook salmon or bay shrimp may find it easier to detect the mouth of the estuary when flow is high than when it is low, but there is no evidence to support this.

Downstream movement of the eggs and early larvae of anadromous species such as striped bass and American shad depends on flow velocities in the rivers and through the Delta (T5a).

Upstream movement of bay shrimp and starry flounder may depend on gravitational circulation, and therefore may increase strongly with seaward X_2 because of the sharp increase in gravitational circulation with seaward X_2 (T6a; Monismith et al. 2002). A mechanism related to landward transport is retention (T7a). All estuarine organisms run the risk of being swept to sea by the tides and net river-derived flow. This risk is greatest for the smallest organisms because of their limited swimming ability. Many estuarine organisms use tidal or residual currents for retention (e.g., Kimmerer et al. 2002, Bennett et al. 2002), and this retention may increase as X_2 moves seaward. This mechanism may be particularly strong for species that remain near the bottom or that move downward when in high salinity.

Here we estimate the form of dependence of travel time on X_2 to examine the potential role of mortality during transport (T6a), and discuss situations in which the components of these mechanisms might operate. The travel time is from the striped bass spawning ground near the mouth of the Feather River to the LSZ (LSZ), centered on the 2 psu isohaline. The distance to be traveled was broken into two segments: the riverine reach from the spawning ground near the mouth of the Feather River to Rio Vista in the Delta, and the estuarine reach from Rio Vista to X_2. Speed of transport by river flow is approximately a power function of flow (Mount 1995 Eq. 2.1 and 2.4). Sommer et al. (2004) determined mean speed along the Sacramento River from the head of the Yolo Bypass near the mouth of the Feather River to the outlet near Rio Vista. Their data fit a power function:

$$v = 0.006 \ Q_{sac}^{0.7} \tag{3}$$

where v is mean velocity (m s^{-1}) and Q_{sac} is Sacramento River flow (m^3 s^{-1}). For convenience a slight negative curvature (about 1% of the variance in log velocity) is ignored in this function. If this velocity relationship applies over the entire distance D between the spawning area and Hood, the travel time in days (TT) is then:

$$TT = 1.91 \ D \ Q_{sac}^{-0.7} \tag{4}$$

The relationship between Sacramento River flow and X_2 is complex, depending on a variety of other factors including export flow and Yolo Bypass flow. However, over a limited range of X_2 values we found that the relationship between Sacramento River flow and X_2 was nearly log-linear. We inserted that relationship into equation 4 to obtain travel time as a function of X_2:

$$TT = 3 \times 10^{-6} \ D \ X_2^{\ 2.1} \tag{5}$$

A particle-tracking model based on the DSM2 Delta model was run for constant flows and repeating tides for a variety of inflow and export conditions (Kimmerer and Nobriga 2008). A group of 5000 particles was released at several points in the Delta over a 24-hour period. The particles were counted as they passed various points in the estuary. Particle tracking runs were made for with nine values of inflow from 340 to 3400 m^3 s^{-1}, and five values of export flow from 57 to 340 m^3 s^{-1}, in a total of 20 combinations (Kimmerer and Nobriga 2008). We ran the model for 92 days, filtered the output to remove tidal fluctuations, and calculated the time at which half of the particles had passed the Chipps Island control point. We then calculated parameters of a

model relating the log of travel time to the log of X_2 and took antilogs to obtain the relationship between travel time and X_2 as a power function. Finally we calculated travel time to the LSZ by multiplying the travel time from Rio Vista to Chipps Island by the ratio of distances traveled. We also determined travel time from Hood to Rio Vista using PTM results to compare with the calculated travel time from the Feather River to Rio Vista.

The resulting travel times show increases with X_2, consistent with Mechanism T5 (Figure 8). The travel time determined using the data from Sommer et al. (2004) was very short in all cases, at most ~5 days, which is consistent with their estimate of hydraulic residence time. The travel time from Hood to Rio Vista based on the particle tracking model was lower than the travel time from the Feather River at high flow (low X_2) but increased more rapidly and was much higher at low flow. This is probably due to tidal effects and alternative pathways which were not included in the calculations of Sommer et al. (2004). In any case the travel time from Rio Vista to the LSZ was much longer than either of the other travel times, because of increasing tidal effects and an increasing channel cross-section below Rio Vista. Travel time began to decrease as X_2 moved above ~ 89 km because the distance from Rio Vista (River Kilometer 100 km) to X_2 was shrinking.

Mortality may be higher in the rivers than the LSZ due to higher rates of visual predation in less-turbid water, or due to the physical rigors of transport of eggs and early larvae. There may also be ways that mortality could increase with decreasing flow (T5b), at least in the rivers. These are discussed below under species-specific considerations, and the mortality rate of striped bass is calculated based on its X_2 relationship and these travel time results.

We are preparing an equivalent analysis of transport up the estuary for species that recruit from the ocean (T6a). Such landward transport can be seen in the near-bottom drifter studies of Conomos (1970). Landward transport by gravitational circulation presumably also scales as a power function of X_2 because of the effect of a seaward increase in mean depth resulting in a greater tendency to stratify than expected by theory (Monismith et al. 2002). Particle-tracking studies using the TRIM3D model are being conducted to test this mechanism and these should provide insight. However, if these studies show that speed of transport increases with seaward X_2, we will still need to model and then measure the extent to which mortality during transport exceeds mortality in the rearing area.

Mechanism Q: Water quality includes effects of contaminants, direct effects of salinity, and suspended sediments. Contaminant effects might involve dilution by high flow, but this is not consistent with the available evidence. Pesticides generally are brought into the estuary by rainfall events, and concentrations of particle-bound pesticides in the estuary are highest following the first flush of the wet season (Bergamaschi et al. 2001; Kuivila and Foe 1995; Whitehead et al. 2004). Loading of methylmercury is higher during runoff events than at other times (Domagalski 2001), and selenium loading from increases with increasing flow (Cutter and Cutter 2004). Furthermore, some of these inputs have changed markedly during the last 10-15 years (Cutter and Cutter 2004), without apparent effects on the X_2 relationships. Thus, although toxic contaminants may exert important controls on some species and life stages (Whitehead et al. 2004), these effects are unlikely to decrease with increasing flow.

Salinity is generally considered an important source of stress for estuarine organisms, but it really is stressful only for benthic and shoreline organisms (Laprise and Dodson 1993). Shifts in salinity as caused by an increase in outflow can cause osmotic stress to benthic organisms, such that the boundary between brackish-tolerant and freshwater benthos shifts seaward (QF2a). To the extent that this leads to reduced benthic grazing, it may provide a mechanism by which abundance at lower trophic levels increases (QF2b). The drought in 1976-1977 resulted in low phytoplankton biomass and low zooplankton abundance in Suisun Bay, which was attributed to the landward range expansion of marine benthic filter-feeders (Nichols 1985). This mechanism may not be as strong as it once was since the overbite clam *Corbula amurensis* is tolerant of both marine and brackish conditions (Alpine and Cloern 1992) and its range overlaps with that of the freshwater clam *Corbicula fluminea*. A weakening of this mechanism because of this introduction should have resulted in a change in slope of the X_2 relationships, which did not occur (Figure 2). Therefore this mechanism does not appear to be important in the San Francisco Estuary.

Turbidity is an important attribute of habitat of some estuarine fish, and young delta smelt and striped bass in particular are more abundant in turbid water than clear water (Feyrer et al. 2007). Turbidity is generally higher in the LSZ than in other parts of the estuary, and increases somewhat as flow increases and X_2 moves seaward (Kimmerer et al. 1998). Turbidity and low light are associated with reductions in success of visually-foraging fish (Breitburg 1988, Chesney 1989), although studies in real foodwebs can reveal surprising interactions (Cuker 1993). This reduction may be greater for piscivores than planktivores, making turbid environments favorable to smaller fish (DeRobertis et al. 2003). If that is true, then increases in turbidity due to increasing flow may reduce predation rates on planktivores, or it may reduce the risk of attack by visually-feeding piscivores such that planktivores can devote more time to foraging and less to predator avoidance. Either should result in better survival of age-0 fish and consequently stronger year-classes when the water is turbid, which generally is associated with high flow.

Previous analyses of suspended sediments in various parts of the estuary have revealed the importance of variability at the tidal time scale, and of bathymetric features, with a small influence of flow (Schoellhamer 2001). The link between suspended sediments and secchi depth is not particularly strong, but secchi depth probably gives a better indication of conditions for visual predation than suspended sediments measured at the bottom. Secchi depth should be linearly related to visual detection range for a given predator and prey, and also can be used to calculate light extinction coefficient so that light levels in the water column can be determined.

We explored the implications of limited light in the water column using a simple predator-prey model (Appendix A). The conclusion of this investigation is that, in contrast to previous assertions in the literature (DeRobertis et al. 2003), there does not seem to be a visual refuge for planktivores irrespective of the water's turbidity. This finding contrasts with the observation that turbidity is an important attribute of habitat as defined by where fish are found (Feyrer et al. 2007). There may be fundamental flaws in how this model is applied, and in particular it might be useful to extend the model to the case in which planktivorous fish form schools, which would require an individual-based model. Clearly it is also essential to learn more about the behaviors of planktivorous and piscivorous fishes in this turbid environment.

Mechanism H: Quantity and quality of habitat may vary with X_2 or flow. The quantity of habitat can be defined in terms of area or volume. Habitat quality can be defined to include variables such as salinity, temperature, turbidity, and depth. Habitat quality can also be defined to include all of the above considerations (e.g., contaminants, food supply), but for the purposes of this discussion we limit it to physical and geographic attributes to distinguish mechanisms related to static descriptions of physical state from the more dynamic attributes already discussed. Generally for estuarine species, salinity is the dominant variable determining large-scale spatial distribution (Kimmerer 2004), whereas smaller-scale distributions may be affected by such factors as bathymetry, turbidity, velocity, or biotic interactions.

The most obvious potential mechanism for an X_2 effect is an increase in quantity of or access to habitat, defined on the basis of salinity, depth, etc., as X_2 decreases. The clearest such example is the sharp increase in splittail abundance during very high-flow years. This increase is apparently due to the increase in spawning or foraging habitat that becomes available when floodplains are inundated, increasing shallow habitat by orders of magnitude (Sommer et al. 1997, Moyle et al. 2004). This effect is nonlinear and essentially a threshold effect, although as discussed previously threshold effects can be smoothed through averaging (e.g., see Figure 2 G). Effects occurring in floodplains are probably not confined to the floodplains, which export organic matter and organisms to subsidize other regions (Sommer et al. 2001).

In addition to floodplain inundation, it is reasonable to expect changes in extent of habitat as defined by salinity to be related to X_2. Freshwater habitat must increase, and marine habitat must decrease, with a seaward X_2. Intermediate salinity ranges may increase or decrease, but the scope for such changes is limited. In any case, a change in habitat area or volume is likely to result in a proportional change in abundance of a species that is habitat-limited.

This class of mechanisms has been investigated using the hydrodynamic model TRIM3D to provide the spatial and temporal coverage of salinity distributions with X_2 (Kimmerer et al. in prep., attached as Appendix B). The model was used to provide tables of volume or area at various combinations of depth and salinity for five scenarios of constant freshwater flow and repeating tides. Available abundance data from all of the fish sampling programs was then explored to develop relationships between abundance or frequency of occurrence and either salinity or salinity and depth together. These two data sets were combined to produce indices of habitat for each species from each sampling program and relating these to X_2, then comparing these relationships with the observed X_2 relationships.

Only for American shad and striped bass did the habitat volume vary with X_2 in a similar way to the abundance indices. The X_2 relationship for the abundance index of longfin smelt (Figure 2) was much steeper than the corresponding relationship of habitat to X_2. Conversely, relationships of habitat to X_2 for bay shrimp and starry flounder had zero slopes, contrasting with the significant slopes of the X_2-abundance relationships (Figure 2). These findings generally are consistent with earlier analysis of the spatial distributions of longfin smelt (Kimmerer 2002a), which did not increase in spatial extent as X_2 moved seaward. They are inconsistent with the finding that the distribution of young striped bass also did not expand with seaward X_2 (Kimmerer et al. 2000).

These analyses considered only salinity and depth, and excluded such attributes as turbidity, an important characteristic of habitat for some estuarine species (Feyrer et al. 2007). It was not possible to model turbidity in the same way that salinity could be modeled. More recent analyses show evidence of an increase in habitat for delta smelt with increasing flow if turbidity is taken into account (F. Feyrer, unpublished).

Several alternative habitat-based mechanisms remain rather speculative (Table 4, Figure 4). The range of habitat as defined by salinity may move from a deep, narrow channel to a region adjoining either shallow vegetated or unvegetated habitat or marshes. This may result in the availability of additional prey refuge for small organisms in the shallows, or additional foraging opportunities. There could also be a juxtaposition of the salinity range of a species with other bathymetric features that add complexity to the habitat, which generally may increase feeding opportunities or cover. Furthermore, tidal velocities increase to seaward, increasing tidal stirring; a seaward X_2 may place a given salinity range in an area of stronger mixing with resulting increases in contact rates with food or, seen another way, increased hydrodynamic complexity of the habitat.

Species-specific considerations

Some potential mechanisms may depend on specific attributes of species, and it may be possible to isolate the life stage during which a given mechanism acts. Species with similar spatio-temporal distributions and life stages may be affected by similar mechanisms. Here we discuss life history characteristics and explore specific mechanisms that may apply to each species, and attempt to delineate the life stage and locations of these mechanisms (Figure 3). This is not meant to be exhaustive, but rather to identify the mechanisms most likely involved in X_2 relationships for these species. More thorough discussion of the biology of several key species can be found in recent documents (e.g., Moyle et al. et al. 2004, Bennett 2005, Rosenfield and Baxter 2007, and the POD synthesis report, http://www.fws.gov/sacramento/es/documents/POD_report_2007.pdf).

Figures 5-7 describe the logic involved in assessing each mechanism as it might apply to four species. Each figure shows several potential mechanisms for one or more species, a study that could be done initially to assess the likelihood that the mechanism is important to that species, the metric that would have to be tested to see if the mechanism actually operates, and a subsequent study to be done if the mechanism appears to operate.

Bay Shrimp Female shrimp *Crangon franciscorum* (Figure 5) spawn in the ocean and the offspring enter the estuary as juveniles during spring (Hatfield 1985). As with many other estuarine decapod crustaceans, the young shrimp make their way up the estuary and generally are most abundant near the LSZ. Late juvenile and adult shrimp in the LSZ remain near or on the bottom, rising off the bottom on both strong floods and ebbs (Kimmerer et al. 2002). This life history limits potential X_2 mechanisms to the juvenile-adult stages, and the locus of the mechanism to the entrance of the estuary, the lower estuary, or the LSZ (Figure 3). The habitat analysis (Kimmerer et al. in prep.) fails to support mechanism H1, at least insofar as habitat can be described by salinity and depth. More promising mechanisms for a species that enters the

estuary from the ocean relate to the strongly asymmetrical residual flow that occurs with a seaward X_2. Therefore likely mechanisms are: T4, the proportion of the young shrimp population that moves into the estuary increases as X_2 moves seaward because of an increasing low-salinity signal inducing migratory behavior; and T5, increasing gravitational circulation increases the rate of landward movement of young shrimp.

Starry flounder (Figure 4) has a somewhat similar life history to bay shrimp but the young disperse further up the estuary, and some are even collected at the south Delta fish facilities (Baxter et al.1999). Juvenile flatfish including some flounder are known to remain near the bottom and undertake tidally-oriented migration off the bottom to move in a selected direction (Harden Jones 1978). Thus, the mechanisms most likely to be important for starry flounder are similar to those for bay shrimp.

Pacific herring abundance is unrelated to X_2. Survival from egg to young-of-the-year was weakly related to X_2 (Kimmerer 2002a), but this relationship is not significant and is now weaker than it was. Herring spawn in mid- to late winter on pier pilings, rocks, and vegetation in Central Bay. Maximum hatching success occurs at a salinity of around 16 (Alderdice and Hourston 1985, Cherr and Pillai 1994). Larvae rear mainly in San Pablo Bay and may be food limited some of the time (Gartside 1995). Juvenile herring rear in the estuary at a mean salinity of about 20 psu during the first few months. Thus both hatching success and rearing depend on reduced salinity, and in particular hatching success requires reduced salinity in Central Bay, since there is little suitable habitat in other areas of the estuary. This is consistent with mechanism H5, with one of the key habitat attributes being substrate for spawning. Rearing habitat may also be weakly related to X_2 (Kimmerer et al. in prep.). Since the X_2 relationship is weak at best, and clear mechanisms exist to explain why herring recruitment should vary positively with flow, no further investigation is needed for the X_2 relationship of herring.

American shad spawn in freshwater in the Sacramento River basin, essentially overlapping with striped bass. The distribution of juvenile shad is rather different from that of striped bass, though, in that the center of the distribution moves seaward through the estuary as the fish grow (Baxter et al. 1999). This distribution implies that several different mechanisms could be operating; together with the rather weak X_2 relationship of this species, this suggests that American shad may not be the best fish to start investigating. Volume of habitat and abundance index had X_2 relationships with a similar slope, consistent with habitat volume being the predominant mechanism (Kimmerer et al. in prep.). On the other hand, upstream effects are likely to be important given the spawning distribution of this species. We suggest no further investigation of the X_2 mechanism(s) of American shad, except in connection with other studies.

Delta smelt are unusual among estuarine-dependent species in having no statistically significant X_2 relationship. This may allow for some productive comparisons with longfin smelt. Nevertheless, there are indications that delta smelt do respond positively to freshwater flow (Feyrer et al. 2007). Delta smelt spawn adhesive eggs most often in the freshwater Delta. Larvae move toward the LSZ during development and juveniles and early adults are concentrated there. Delta smelt are probably the most vulnerable of any of the species discussed here to export pumping, given their distribution during early life. However, their vulnerability is related to X_2, and few delta smelt reach the salvage facilities during wet periods (Kimmerer in

press). The proportion of the juvenile population lost to export pumping had a similar slope with X_2 as the abundance- X_2 relationship in the summer townet survey after 1981 (Figure 2). However, this similarity owed a lot to the large confidence limits on the estimates, and this mechanism fails to explain the change in slope of the X_2 relationship or the lack of such a relationship in the fall midwater trawl survey, which is considered the most suitable survey for estimating delta smelt abundance.

Current research is focusing on the potential interactions among turbidity, flow pulses, and distribution of the smelt, particularly in fall to winter. These investigations go beyond the rather crude scale of the X_2 relationships, but may provide useful information for understanding those relationships.

Longfin smelt (Figure 5) have the strongest X_2 relationship of any species in the estuary, and also the relationship that changed the most clearly, with a decrease of about 5-fold in abundance for any given X_2 value. Longfin smelt spawn adhesive eggs in Suisun Bay and the western Delta during winter. Larvae and juveniles disperse rapidly into San Pablo Bay and further seaward (Rosenfield and Baxter 2007), but beginning at the later larval stage these fish begin tidal migrations (Bennett et al. 2002) consistent with attempts to remain within the estuary. These findings seem somewhat contradictory.

Because of the strong relationship with X_2, this species should be amenable to investigations into mechanisms, several of which seem likely. As with delta smelt the spawning habitat of this species is unknown, so the variation in spawning habitat with flow cannot be investigated. Transport from spawning areas to rearing areas may be affected by flow (T5), although it seems unlikely that survival is better in rearing areas than in the more turbid LSZ. The spatial extent of habitat for this fish is very broad, encompassing essentially the entire estuary below the LSZ (Kimmerer 2002b) and even the coastal ocean (Rosenfield and Baxter 2007), although the distribution is weighted toward low salinity in the early life stages. Habitat quantity was negatively related to X_2 but with a much smaller slope (Kimmerer et al. in prep.), implying that the increase in habitat with flow (Mechanism H1) is insufficient to explain the X_2 relationship of longfin smelt.

The contrast between longfin and delta smelt may depend on the location of the fish during rearing. Delta smelt are more closely associated with the LSZ than are longfin smelt. This implies that the mechanism for the relationship of longfin smelt to X_2 may depend on conditions over a broader region than the LSZ. Nevertheless, longfin smelt larvae are frequently found near the south Delta export facilities (Dege and Brown 2003), so mechanisms involving export flow may be important to these fish.

A retention mechanism related to gravitational or lateral residual circulation is one plausible candidate to explain the strong X_2 relationship of longfin smelt (T7). Abundance patterns from the Bay study otter trawl showed a peak at around 20 psu salinity, whereas the peak from the Bay study midwater trawl through the whole water column was around 5 psu (Kimmerer et al. in prep.). This difference suggests that longfin smelt remain deep in the water column when they reach higher salinity. Such a pattern would result in retention, which should increase as X_2 moves seaward because of the increased strength of gravitational circulation.

Splittail increase sharply in abundance when floodplains are inundated, and the area of physical habitat (H1) for spawning, rearing, or possibly adult foraging appears to be the key (Sommer et al. 1997, 2004, Moyle et al. 2004). Food supply is higher but growth of young splittail is not higher in floodplains than elsewhere, implying that the key process may be feeding of spawning adults (Feyrer et al. 2007b). This is a good example of an X_2 mechanism related to physical habitat, but one that is unrelated to the actual LSZ habitat that X_2 indexes.

Striped bass (Figure 6) survival from egg to young-of-the-year (YOY) varies strongly with flow or X_2 (Kimmerer 2002a, Figure 2). The slope of the relationship of survival from egg to 6mm larva with X_2 was identical to that for egg-YOY survival (Kimmerer et al. 2001). Furthermore, survival from 6mm to YOY was unrelated to flow or X_2. This implies that the mechanism for the striped bass X_2 relationship occurs during early life, particularly during transport down the rivers (T5). An alternative mechanism arises because some striped bass spawn in the lower San Joaquin River (Turner and Chadwick 1972). Eggs and larvae spawned in this region are unlikely to be transported to the LSZ under low-flow conditions and may be lost to export pumping (T1).

CDFG (1992, p. 13) hypothesized that low flow in the Sacramento River resulted in poor survival of striped bass eggs because they would sink to the bottom, presumably succumbing to low oxygen or physical damage. If true this would be consistent with mechanism T5. If mortality during transport down the rivers does not depend on flow, survival could still be a function of X_2 if mortality in the rivers were higher than that in the LSZ. The slope of the X_2 regression for survival was -0.027 (Kimmerer 2002a). Although the relationship between travel time and X_2 is weakly nonlinear, the average slope is about 0.08 (Figure 6). This implies an added daily mortality rate of 0.33 d^{-1} in the river (0.027 / 0.08). According to Rose and Cowan (1993), the maximum daily mortality rate of striped bass is on the order of 0.2 d^{-1}. Although the mortality calculated from the X_2 relationship and travel time is rather high, these results do not allow this mechanism to be ruled out; nevertheless they suggest that a field program may be able to detect the elevation in mortality by this mechanism.

The habitat mechanism (H1) is a reasonable alternative for striped bass. The slope of habitat quantity vs. X_2 was similar to that for survival and abundance (Kimmerer et al. in prep.). This offers a clear contrast to the transport mechanisms that could be resolved, at least in part, by a key set of investigations into the transport issue (Figure 7).

Research Plan

In developing the research plan we must consider other ongoing related efforts. The one with the greatest potential impact on this plan is the Pelagic Organism Decline (POD) effort (Sommer et al. 2007). A recent report (POD Synthesis Team 2007) describes the current state of the POD studies and highlights the results of some ongoing research. That effort is more comprehensive, more urgent, and more limited in geographic scope than what is proposed here. Thus, our best strategy is to integrate our plan with the POD effort.

The POD itself causes some difficulties in investigating mechanisms underlying the X_2 relationships. First, abundance of some species is at an all-time low, so monitoring collects fewer specimens for analysis and abundance estimates have wider confidence limits. Second, sampling for some programs has been stopped to protect delta smelt, so it may not be possible to carry out the analyses required to reveal X_2 mechanisms for other species. Third, the relationships themselves have changed in a few cases: those for longfin smelt and striped bass now have much lower responses than before (see above). And finally, the intensity of focus on the Delta will limit funding for activities outside the Delta, where some of the more tractable mechanisms may operate.

Although some of the X_2 relationships including those of some POD species have changed since 2001 (Figure 2), most of the changes involve a change in mean value rather than in slope (although longfin smelt in 2007 may be an exception). This means that the way the various populations respond to flow and its correlates has not changed, but that each population is responding at a lower level. This is a similar response to that observed after the 1987 decline in food supply to the upper estuary due to the introduction of *Corbula amurensis*.

There is also a general effort toward resolving environmental problems in the Delta, triggered by the realization of the vulnerability of the Delta to seismic and flood hazards (Mount et al. 2006). This is likely to result in significant changes to the physical configuration of the Delta, possibly including a peripheral canal that would route freshwater from the Sacramento River around instead of through the Delta. The original X_2 relationships are empirical and therefore based on the current configuration. Changes to that configuration may alter these relationships but it is not possible to say how. Although understanding the mechanisms behind the X_2 relationships might help to forecast how they may change with changes in configuration, it is possible the relationships themselves could be altered or destroyed by such a change in configuration.

Principles   The following principles are essential for designing a research and monitoring program for the X_2 relationships.

Compare mechanisms using weight of evidence. It is not possible to use a traditional hypothetico-deductive framework for assessing the importance of alternative mechanisms. The detection of "significant" relationships is nearly irrelevant to our purpose. Rather, we seek to determine which mechanisms are most likely contributors to the relationships. These comparisons might ultimately be amenable to formal comparisons using Bayesian approaches, but initially the weight of evidence should be used. This should investigate whether each prospective mechanism is consistent with the relationship and with other information. If other mechanisms are also consistent with the observed relationship, it may not be possible to determine rigorously which is the more important, but it may not matter if both contribute.

In previous sections we examined some of the potential mechanisms for the X_2 relationships. The analysis of physical habitat showed that for American shad, the slope of the X_2 relationship for the abundance index was similar to that for habitat volume. This is consistent with the interpretation that abundance of American shad is limited by habitat as defined by salinity, and that variation in the quantity of this habitat with X_2 controls abundance. This does not mean that this is a correct explanation. However, if alternative explanations were investigated and found

inconsistent with the X_2-abundance relationship of American shad, it would lend further weight to the habitat model.

By contrast, the slope of abundance of longfin smelt to X_2 is much too steep to be explained by the habitat model, at least in its current rudimentary form. This does not mean that increasing habitat volume with seaward X_2 does not contribute to the increase in abundance (before or after POD), but that the contribution is modest and the key factor is likely to be something else. As an additional contrast, the two ocean-spawning species, bay shrimp and starry flounder, had no relationship of habitat volume to X_2, so other explanations must be sought.

Build on what is already known. There is a good deal of monitoring data, good hydrodynamic models, and considerable information on many of the target species. Some evidence is available to support or refute some mechanisms, or to refine them to the point where key measurements can resolve one or more mechanisms.

Conduct key studies that separate the realm of possibilities. For some species the range of possible mechanisms is broad, but they fall into categories. For example, if otolith studies reveal that the early growth of longfin smelt is independent of X_2, then early transport and first feeding could be downgraded as possible contributors to the X_2 mechanism, and subsequent focus would be on later stages of the life cycle.

Make the program adaptive, not comprehensive. Even where we do not have particularly good information about certain mechanisms, it is not necessary to try to address all of them at once or in any fixed sequence. Instead, we should select subsets of mechanisms for each species or suite of species that are ripe for analysis, and plan efforts to provide needed information in the next few years. If investigations fail to show that selected mechanisms are operating, then we should go to the next most likely mechanism(s).

Combine directed studies with the solicitation process for specifics. Some of the needed studies are so specific that they could be undertaken as directed actions by the agencies or other entities. However, scientific research generally is a collective effort by many people, none of whom individually have all the knowledge needed for a particular objective. The more people that can be intellectually engaged in a project, the better. Although this can take the form of workshops and meetings, the most effective way of developing ideas for research projects is through solicitation for proposals. If the solicitation makes the objectives clear, the most likely result will be one or more proposals with novel, creative approaches to the problem.

Consider economies of scale. For example, a potential mechanism that may involve more than one species should be preferred over one that applies only to one species, all else being equal.

Do the easy things first, but begin the long-term studies soon. Some of the mechanisms could be further refined or even tested by data analysis and simulation modeling. This has been started and has already produced results. However, some more labor- and time-intensive studies will most likely be necessary irrespective of the outcome of the analysis and modeling. The sooner these studies start the more likely they will provide results in a reasonable time frame.

Classes of studies needed   Referring to Figures 5-7 for guidance, it is apparent that most of the data analyses and many of the model studies that would support investigation of X_2 mechanisms for these species have already been done or are underway. Thus, it will be necessary to conduct field and laboratory studies to make progress on these mechanisms. A few data and modeling studies remain to be completed. The model studies could be made fairly general, so that they could apply to multiple species. The classes of studies are presented in approximate sequence based on the contingencies shown in Figures 5-7.

Data on early life stages. One of the key studies identified above was to distinguish among alternative mechanisms for striped bass in the freshwater parts of the system (Figure 6). Some evidence suggests that the X_2 mechanism for striped bass occurs very early during egg and early larval development (Kimmerer et al. 2000, 2001). A key data set that could provide information on this is that from the egg and larval survey run during 14 years in the the 1970s to 1990s. Although some information has been gleaned from these data (Kimmerer et al. 2001), there is much more that could be learned starting with the raw data. An additional, underexplored data set is that resulting from plankton samples taken during the early years of the Bay Study in the 1980s, which might be useful in at least designing studies of bay shrimp and starry flounder.

Retention models.   All estuarine organisms must somehow overcome net seaward flow to maintain populations within the estuary. Smaller, planktonic organisms including larval fish have swimming speeds that may not suffice for them to maintain position. For these organisms, vertical migration or demersal behavior may prevent them from being washed out of the estuary. However, the range of such migrations that have been observed has been small and apparently insufficient to overcome advection (Kimmerer et al. 1998, 2002, Bennett et al. 2002). This topic is ripe for a model study similar to that used to investigate the entrainment of bay shrimp and starry flounder. The principal questions would be: how does the observed migration behavior play out in the 3-dimensional estuary? And how do changes in freshwater flow and X_2 affect this interaction?

Predation models.   The predation model in Appendix A gives results that do not seem to square with observations, and do not seem to provide enough habitat for planktivorous fish to live in. Obviously this model is wrong, but how?   It is likely that modeling all fish as having the same characteristics over-simplifies the problem and fails to account for nonlinear outcomes of predator-prey interactions that may not be readily apparent. An alternative is to use an individual-based approach to allow for variation in individual behaviors, and to allow for realistic features such as suppression of feeding during times of high predation risk, and for escape responses of prey fish.

Predation studies.   Studies of predation are usually conducted from the perspective of the predator rather than the prey, although there are exceptions (e.g., Lindley et al. 2003). However, the most likely predatory impact connected with the X_2 mechanisms occurs through changes in turbidity. Depending on the outcome of initial model analyses, studies might be designed to determine how predation on, and feeding by, common planktivorous fish (e.g., early life stages of target species) vary with turbidity. This would likely be a combination of laboratory and field studies.

Small-scale spatial distributions. Many of the field/laboratory studies in the diagrams (Figures 5-7) require some knowledge of the fine-scale distributions of the target species and possibly their prey. For example, studies of feeding and predation are most often done at a rather coarse scale of resolution. Fish are collected from one or a group of trawls and their stomachs analyzed for prey abundance. This may then be compared with abundance determined in the field at a different scale, location, or even time of collection. However, Appendix A makes it clear that the relevant spatial scales for predation studies are meters or less. Therefore the first step to be able to conduct such studies would be to resolve the distribution of fish and plankton at finer scales than has been done before. This will likely require alternative sampling methods such as high-resolution video or sonar.

Otolith studies. A lot can be learned about the history of fish from their otoliths, including age, growth rate and history, hatch size, and sometimes even the general location (e.g., which river, salinity) of hatching and development (Hobbs et al. 2007). Otolith-derived histories would be invaluable for assessing the characteristics of surviving individuals including where and when they hatched. This is particularly relevant to unraveling the transport mechanisms (Figures 5-7), to which the key (once the effect of X_2 on rate of movement has been established) is how fast the survivors get to their rearing habitat and how much lower the daily survival is during the trip.

Feeding studies. Note that the need to investigate feeding is contingent on other elements (Figures 5-7) and may not be necessary. Investigations of feeding by organisms with complex life histories and repertoires of behavior can be challenging. Most such studies stop at the point at which the broad outlines of diet are known or, in some cases, some comparison of diet with available prey has been made. This is inadequate for the analysis of feeding in connection with the X_2 mechanisms. In these analyses the question being asked is: does a flow-related increase in food availability cause the observed increase in growth rate? Note that flow-related increases in food quantity have not been detected (Kimmerer 2002a, b). Therefore any increase in growth rate with increasing flow would likely be due either to differences in availability (e.g., through proximity to foraging opportunities in shallows), or to subtle effects of flow on food quantity not detectable in the routine monitoring. This would therefore require some combination of diet analysis, bioenergetic modeling, and possibly individual based modeling to fully explore these possibilities.

Population dynamics. The results of otolith studies and analyses of feeding, predation, and mortality should be placed in the context of population dynamics. This requires a better understanding of the full life history of the species, or the part of the life history in the estuary. The extant sampling programs do not collect all life-history stages of any species. If other studies get to the point where the results can be interpreted only through population dynamics, some additional short-term monitoring may be warranted. The Egg and Larval survey was an example of a limited-term monitoring program designed for a specific purpose, although the data were never fully explored (see above). A possible example for the X_2 program would be that investigations of the survival of bay shrimp during movement up the estuary would need to include monitoring of early life stages throughout the estuary using finer-mesh nets than have previously been used.

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Table 1. Physical changes in the estuary resulting from an increase in freshwater flow.

Number	Change	Description	References
1	Stage, velocity	Increase	
2	Floodplain inundation	Increases	Sommer et al. 1997
3	Sediment loading	Concentration and loading increase.	Krone 1979, Wright and Schoellhamer 2004
4	Nutrient loading	Concentration may decrease, but loading increases	Nixon 2003; Nixon et al. 1986
5	Organic matter loading	Same	Jassby and Cloern 2000
6	Contaminant loading	Same; generally freshwater flow does not dilute contaminants but may increase runoff, e.g., of pesticides.	Bergamaschi et al. 2001; Kuivila and Foe 1995; Luoma and Cain 1979
7	Organism loading	Planktonic organisms and small fish are moved downstream more rapidly in rivers and through Delta.	Brandes and McLain 2001
8	Migration cues	May be clearer for anadromous salmon seeking the ocean or the river.	
9	Diversion losses	Lower fraction of inflow diverted, lower proportion of substances and some organisms	Turner and Chadwick 1972, Kimmerer in press
10	Residence time	Residence time of water decreases as flow increases; residence time of organisms or particles usually decreases.	Walters et al. 1985
11	Net flow and transport	Net flow through the estuary is due to river flow.	
12	Extent of salinity field	Decreases	Jassby et al. 1995
13	Salinity at any point	Decreases	
14	Turbidity at any salinity	Increases somewhat	This report
15	Location of any salinity range	Moves seaward and may be adjacent to different bathymetry	
16	Volume or area of any salinity range	May increase or decrease; freshwater region must increase, most saline decrease	Kimmerer et al. in prep.
17	Stratification	Increases due to compression of salinity field, but water depth is a key factor	Monismith et al. 2002
18	Gravitational circulation	Increases with increasing stratification and compression of the salinity field	Schoellhamer 2001, Monismith et al. 2002
19	Ocean-estuary exchange	Increases because of tidal pumping; exchange of organisms may be sensitive.	Fram et al. 2007; Martin et al. 2007
20	Tidal mixing	Mixing within a salinity range increases as that range moves seaward	

Table 2. Summary statistics for X_2 relationships based on species and sampling programs represented in Figure 2 (bold) and the same species from other sampling programs. Sources of the data are: T, summer townet survey; M, fall midwater trawl survey; B, Bay study midwater trawl; O, 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 X2, and the slope with 95% confidence limits for a step function in 1987-1988. Significant parameters ($p < 0.05$) are in italics. Step functions with p values > 0.1 are not included. The fit to the delta smelt townet data required an interaction between the X2 value and a step change in 1981-1982 (Kimmerer 2002). The fit to striped bass survival and abundance indices had step change in 1995-1996, and data before 1978 were excluded. Values presented here are X2 slopes for the individual time periods.

Species	Source	N	p	Intercept	X_2	Step
Bay shrimp	*O*	26	<0.0001	3.7	*-0.02 ± 0.01*	
Starry flounder	O	27	0.0006	4.7	*-0.03 ± 0.02*	*-0.64 ± 0.45*
Pacific herring	B	26	0.09	2.5	0 ± 0.02	*-0.49 ± 0.44*
American shad	M	38	0.004	4.0	*-0.013 ± 0.009*	*0.21 ± 0.20*
American shad	B	25	0.004	4.9	*-0.018 ± 0.012*	
Longfin smelt	M	38	<0.0001	7.0	*-0.05 ± 0.01*	*-0.81 ± 0.28*
Longfin smelt	B	26	0.0001	8.0	*-0.06 ± 0.03*	*-0.75 ± 0.60*
Longfin smelt	O	27	<0.0001	8.1	*-0.06 ± 0.02*	*-0.46 ± 0.36*
Delta smelt	T	20	0.018	-0.3	*0.022 ± 0.017*	
Delta smelt	T	25	0.38	0.9	-0.007± 0.016	
Delta smelt	M	38	0.14	2.6	0.001 ± 0.01	-0.277 ± 0.278
Delta smelt	B	26	0.6	3.1	-0.007 ± 0.03	
Splittail	M	38	0.0002	3.0	*-0.028 ± 0.013*	
Splittail	B	26	< 0.0001	4.70	*-0.04 ± 0.017*	
Striped bass (survival)	T*	32	<0.0001	4.6	*-0.025 ± 0.011*	*-0.79 ± 0.30*
Striped bass	T	44	<0.0001	2.5	*-0.019 ± 0.015*	*-1.18 ± 0.31*
Striped bass	M	38	<0.0001	4.1	-0.011 ± 0.014	*-0.90 ± 0.31*
Striped bass	B	26	0.0006	5.8	*-0.027 ± 0.020*	*-0.93 ± 0.44*
Striped bass	O	27	0.0001	5.2	*-0.016 ± 0.012*	*-0.73 ± 0.27*

Table 3. X_2 relationships for threadfin shad from the fall midwater trawl, and species collected in the San Francisco Bay Study, but not included in Table 2. Where age class is not given all data were used. Source is either Differences between this and results from the Bay Study in Table 2 are the use here of a constant averaging period for X_2 and variable year for the step function. Starry flounder in this table is age-0, whereas that in Table 3 is age-1 with X_2 lagged 1 year. Parameters with confidence limits excluding zero are in italics.

Species	Age Class	Source	N	P	R^2	Intercept	Step after Year	X_2	Step
Brown smoothhound	0	M	27	0.026	0.26	2.15	1998	0.012 ± 0.012	-0.25 ± 0.30
Leopard shark	0	M	27	0.0019	0.41	1.78	1984	-0.005 ± 0.01	*-0.52 ± 0.29*
Pacific herring	0	M	26	0.052	0.23	2.69	1989	-0.003 ± 0.02	*-0.51 ± 0.41*
Threadfin shad		FMWT	25	0.8	0.0	3.73	1991	-0.002 ± 0.01	*0.57 ± 0.52*
Threadfin shad		M	25	0.00023	0.53	5.23	1991	*-0.038 ± 0.02*	*0.57 ± 0.52*
Northern anchovy		M	26	0.015	0.31	3.93	2000	-0.002 ± 0.007	*-0.28 ± 0.18*
Plainfin midshipman	0	M	27	0.00015	0.52	3.32	1985	0.007 ± 0.014	*0.84 ± 0.36*
Jacksmelt	0	M	25	0.0011	0.46	3.52	1987	*0.017 ± 0.015*	*-0.61 ± 0.34*
Topsmelt	0	M	20	0.13	0.21	3.09	1984	0.003 ± 0.03	*0.64 ± 0.645*
Staghorn sculpin	0	M	27	0.12	0.16	3.93	1998	0.001 ± 0.01	*0.31 ± 0.30*
White croaker	0	M	27	0.005	0.36	3.55	1996	0.01 ± 0.02	*-0.76 ± 0.50*
Shiner perch	0	M	27	0.0028	0.39	4.22	1987	0.002 ± 0.01	*-0.46 ± 0.24*
Walleye surfperch	0	M	26	0.038	0.25	2.93	2000	-0.001 ± 0.02	*0.65 ± 0.50*
Black surfperch		M	27	0.057	0.21	1.21	1995	0.007 ± 0.016	*0.43 ± 0.35*
Barred surfperch		M	27	< 0.0001	0.64	2.04	1984	*0.012 ± 0.012*	*-1.0 ± 0.3*
Bay goby		O	27	0.0044	0.36	4.37	1987	0 ± 0.01	*0.47 ± 0.26*
Cheekspot goby		O	26	< 0.0001	0.77	1.20	1988	0.008 ± 0.02	*2.1 ± 0.5*
Yellowfin goby	0	O	27	0.0039	0.37	5.61	2000	*-0.03 ± 0.02*	-0.43 ± 0.48
Pacific pompano		M	26	0.0034	0.39	2.47	1986	0.007 ± 0.02	*0.84 ± 0.48*
English sole	0	O	27	0.034	0.24	3.79	1998	0.008 ± 0.013	*0.41 ± 0.32*
Speckled sanddab		O	27	< 0.0001	0.55	3.80	1991	0.005 ± 0.012	*0.67 ± 0.26*
California tonguefish	0	O	26	0.045	0.24	5.10	1994	-0.024 ± 0.027	*-0.69 ± 0.57*
Crangon nigricauda		O	26	< 0.0001	0.70	1.55	1986	-0.002 ± 0.01	*0.82 ± 0.232*
C. nigromaculata		O	26	< 0.0001	0.63	0.64	1988	0 ± 0.014	*0.918 ± 0.307*

Heptacarpus stimpsoni	O	26	< 0.0001	0.75	-1.42	1988	*0.024 ± 0.014*	*1.122 ± 0.303*
Palaemon macrodactylus	O	26	0.95	0.00	0.57	1999	0 ± 0.008	-0.075 ± 0.206
Cancer magister	O	27	0.0013	0.43	-1.91	1998	*0.057 ± 0.037*	*1.413 ± 0.884*
C. gracilis	O	27	0.0006	0.46	1.12	1990	0.013 ± 0.014	*0.646 ± 0.301*
C. antennarius	O	27	< 0.0001	0.60	0.69	1992	0.014 ± 0.016	*0.993 ± 0.344*
C. productus	O	27	< 0.0001	0.70	0.51	1984	0.004 ± 0.012	*1.201 ± 0.345*

Table 4. Summary of some likely mechanisms for effects of flow on estuarine biota. Mechanisms are identified by class (F = food supply, T = transport, Q = water quality, H = extent of habitat) with a number to identify each mechanism in the text. Some mechanisms identified by two letters include elements of two classes of mechanism (e.g., mechanism TF1b posits that transport of forage organisms to diversions in the Delta reduces food supply for higher trophic levels). The H(F) mechanisms may involve effects of habitat occurring either through predation or through food supply. The column "Table 1" refers to the physical basis for the relationship to flow listed in Table1. Some mechanisms are broken into parts identified by lower-case letters; for example, mechanism F1 includes all parts a, b, and c. References in bold are from the San Francisco Estuary. References in italics either refute or fail to support the mechanism indicated. Mechanisms in bold are "primary" in having some positive support from the San Francisco Estuary.

Class	Mech. #	Table 1	Description	References
F	**F1a**	4	Nutrient loading increases with flow	Nixon 2003; Nixon et al. 1986; Riley 1937
	F1b		Increased nutrient loading stimulates primary production	**McCulloch et al. 1970, Cloern and Jassby 1994, Lucas et al. 1998**
	F2a	17	Stratification increases	Geyer 1993, **Monismith et al. 1996, 2002, Gross et al. in prep.**
	F2b		Increased stratification stimulates primary production	**McCulloch et al. 1970, Cloern and Jassby 1994, Lucas et al. 1998**
	F3a		Ammonium loading from sewage plants is more diluted	**Hager and Schemel 1992**
	F3b		Low ammonium concentration allows rapid diatom growth and production	**Wilkerson et al. 2006, Dugdale et al. 2007**
	F4a	5	Loading of organic matter increases with flow	Day et al. 1994, Smith and Hollibaugh 1993, **Schemel et al. 1996, Jassby et al. 1995, Jassby and Cloern 2000**
	F4b		Increased organic loading stimulates bacterial production	**Hollibaugh and Wong 1996**
	F1c, F2c, F3c, F4c		Increased food production/abundance passed up the foodweb	Aleem 1972, *Kimmerer 2002a, b, 2004, 2005*
T	**T1**	9	Proportion of water and organisms lost to diversions decreases with increasing flow	**Turner and Chadwick 1972, Stevens et al. 1985, Kimmerer and Nobriga 2008**
	T2	15	Lower fraction of populations is vulnerable to diversions when X2 is west of the Delta	**Kimmerer and Nobriga 2008, Kimmerer in press**
	TF3a		Lower diversion mortality on food organisms	None
	TF3b		Higher food availability	None
	T4a	8	Better cues for migration to spawning or rearing habitat	None

	T5a	7	Faster transport by net (river) flow to spawning or rearing habitat	**Turner and Chadwick 1972**
	T6a	18, 19	Faster transport by estuarine residual circulation into the estuary or to spawning or rearing habitat	**Talianchich et al. in prep.**
	T7a	18	Retention within a region of the estuary increases with residual circulation	**Talianchich et al. in prep.**
	T4b, **T5b**, **T6b**, **T7b**		Daily growth is lower or daily mortality is higher outside of habitat than inside	Frenette et al. 1995 Dodson et al. 1989, Wainwright et al. 1996, Sirois and Dodson 2000; *Kimmerer et al. 1998*
Q	Q1	6	Increased flow dilutes contaminants resulting in higher survival.	*Kuivila and Foe 1995, Luoma and Cain 1979, Bergamaschi et al. 2001*
	QF2a	13	Decreased salinity causes osmotic stress shifting benthic community from salt-tolerant toward freshwater	Kaartvedt and Aksnes 1992
	QF2b		Reduced benthic grazing at intermediate salinity increases food supply to higher trophic levels	Wilber 1992, Livingston et al. 2000, **Nichols 1985**, *Alpine and Cloern 1992*
	Q3a	3	Loading of sediment increases with increasing flow	**Krone 1979, Schemel et al. 1996**
	Q3b	14	Turbidity increases in rearing habitats	**This report**
	Q3c		High turbidity reduces rates of capture by visual predators, increasing survival of larvae and juveniles	Monteleone and Houde 1992, Gregory and Levings 1998, *Breitburg 1988*
H	**H1**	16	Quantity (area or volume) of spawning or rearing habitat increases with increasing flow or seaward X_2.	Gammelsrød 1992, Sklar and Browder 1998; **Sommer et al. 1997, 2004, *Kimmerer et al. 2001, Kimmerer 2002b, Kimmerer et al. in prep.***
	H2		Access to spawning or rearing habitat increases with increasing flow or seaward X_2.	**Sommer et al. 1997**
	H(F)3a	15	Overlap of salinity range with shoals increases	None
	H(F)4a	15	Overlap of salinity range with marsh increases	None
	H(F)5a	15	Spawning or rearing habitat increases through overlap of salinity range with other bathymetric features, i.e., "habitat complexity"	None
	H(F)6a	17, 20	Greater tidal mixing or hydrodynamic complexity with seaward X2 increases foraging opportunities or contact rate with food.	None
	H3b, H4b, H5b, H6b		Increased refuge from predators	None
	HF3b, HF4b, HF5b, HF6b		Increased input of food from shallows and marshes	None

Figure Captions

1. Map of the San Francisco Estuary showing major basins and the 10m depth contour. Lines with pairs of letters indicate cross-sections shown in 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, and RV, Rio Vista.

2. $\log_{10}$ abundance indices for fish and shrimp (survival index for striped bass) plotted against X_2 as in Kimmerer (2002; Figure 8). Triangles and solid lines, data up to 1987; circles and dotted lines, 1988-2006; filled circles, 2000-2006 (bay shrimp only through 2005). Gray symbols are transitional POD years 2000-2001. Lines are provided only when statistically significant. Regression statistics in Table 2.

3. Diagram of classes of fish-X2 mechanisms. The first column indicates life stages of a target species (usually a fish). The second indicates what has to change as flow increases for an X2 mechanism to operate at that life stage. The third column indicates what this mechanism would require in order to operate as hypothesized. This can be useful in deciding how to investigate the mechanisms. The arrows on the right show which species are likely to be affected by flow conditions at which life stage and gross location.

4. General logic diagram for mechanisms, explained further in Table 4. Blue shapes indicate direction of change with increasing flow: red is increase, blue is decrease. Rounded rectangles are direct responses to flow (e.g., nutrient loading increases with flow, F1a). Rectangles are intermediate responses (e.g., primary production increases with flow, F1b). Ovals are ultimate responses of target species either in increased growth or increased survival, both assumed to cause increases in population size.

5. Logic diagram for investigating mechanisms pertaining to either bay shrimp or starry flounder. Rounded boxes indicate mechanisms (color coded by class of mechanism), rectangular boxes indicate studies (color coded by type of study), and diamonds indicate decision points. At each decision point if the metric responds as predicted (i.e., the answer is Yes), investigation proceeds to the next step; if not (ND), there may be no reason to proceed with further investigation, as indicated by dashed arrows. Answers in light gray have not been determined, whereas those in black have (see text). The red box indicates a key study that can separate the range of possibilities and help focus attention on one set of likely mechanisms. In this case, the particle tracking model has shown that landward movement of particles that stay near the bottom is faster with more seaward X2, consistent with mechanism T6a for both bay shrimp and starry flounder.

6. As in Figure 5 for longfin smelt.
7. As in Figure 5 for striped bass.
8. Relationship of travel time to X2. Data are from the DSM2 particle tracking model (PTM) or analyses in the Sacramento River (Sommer et al. 2004).
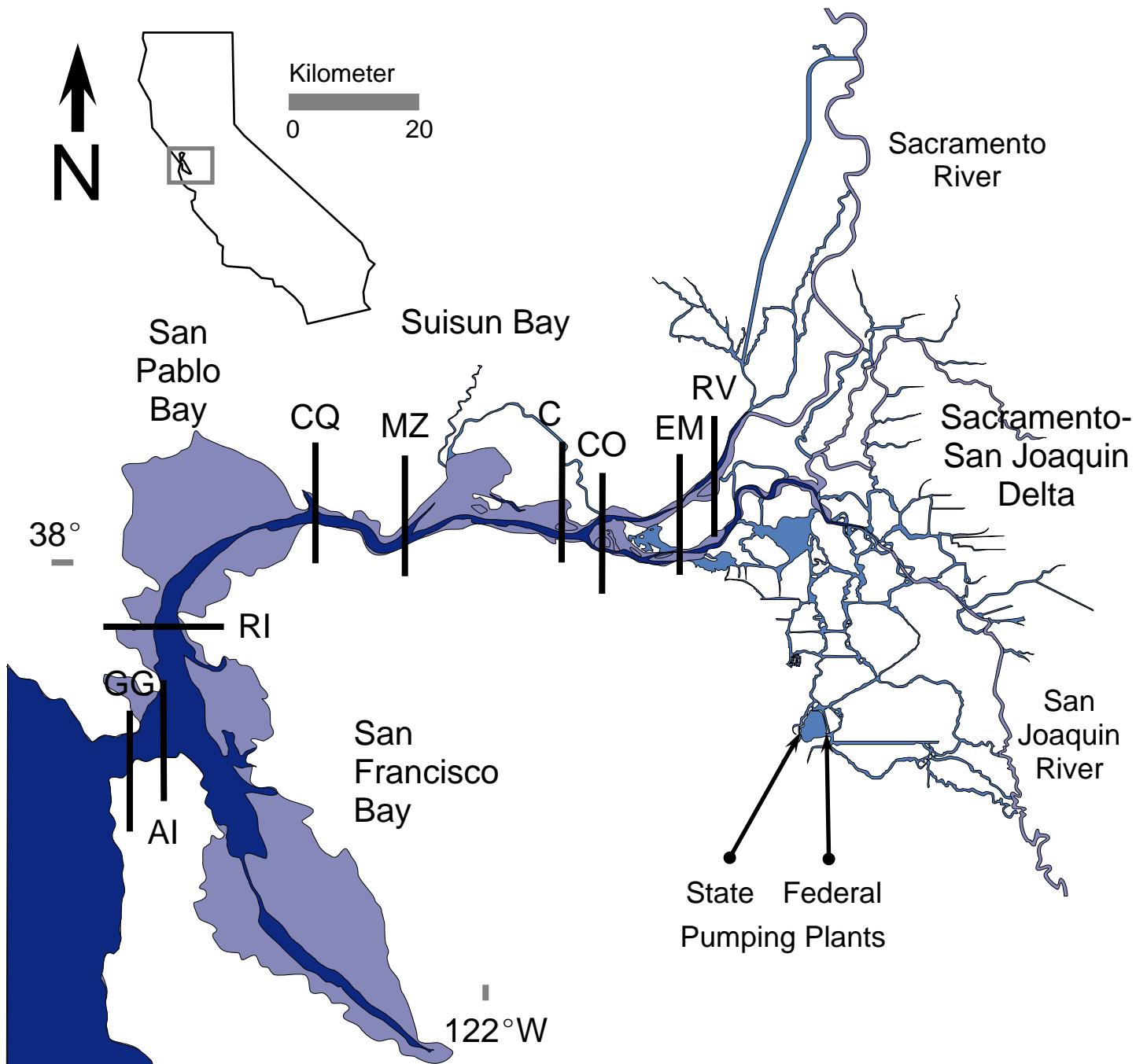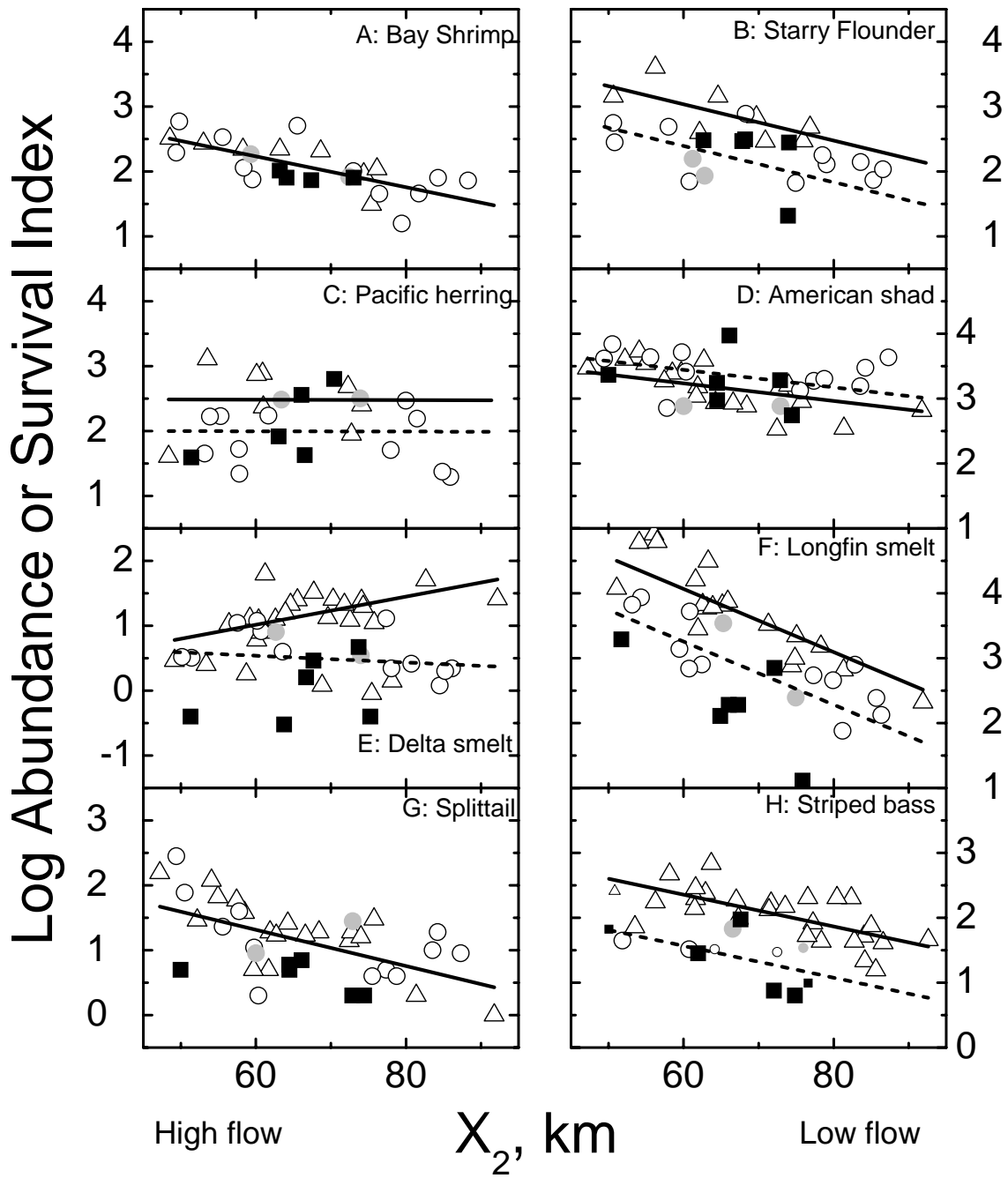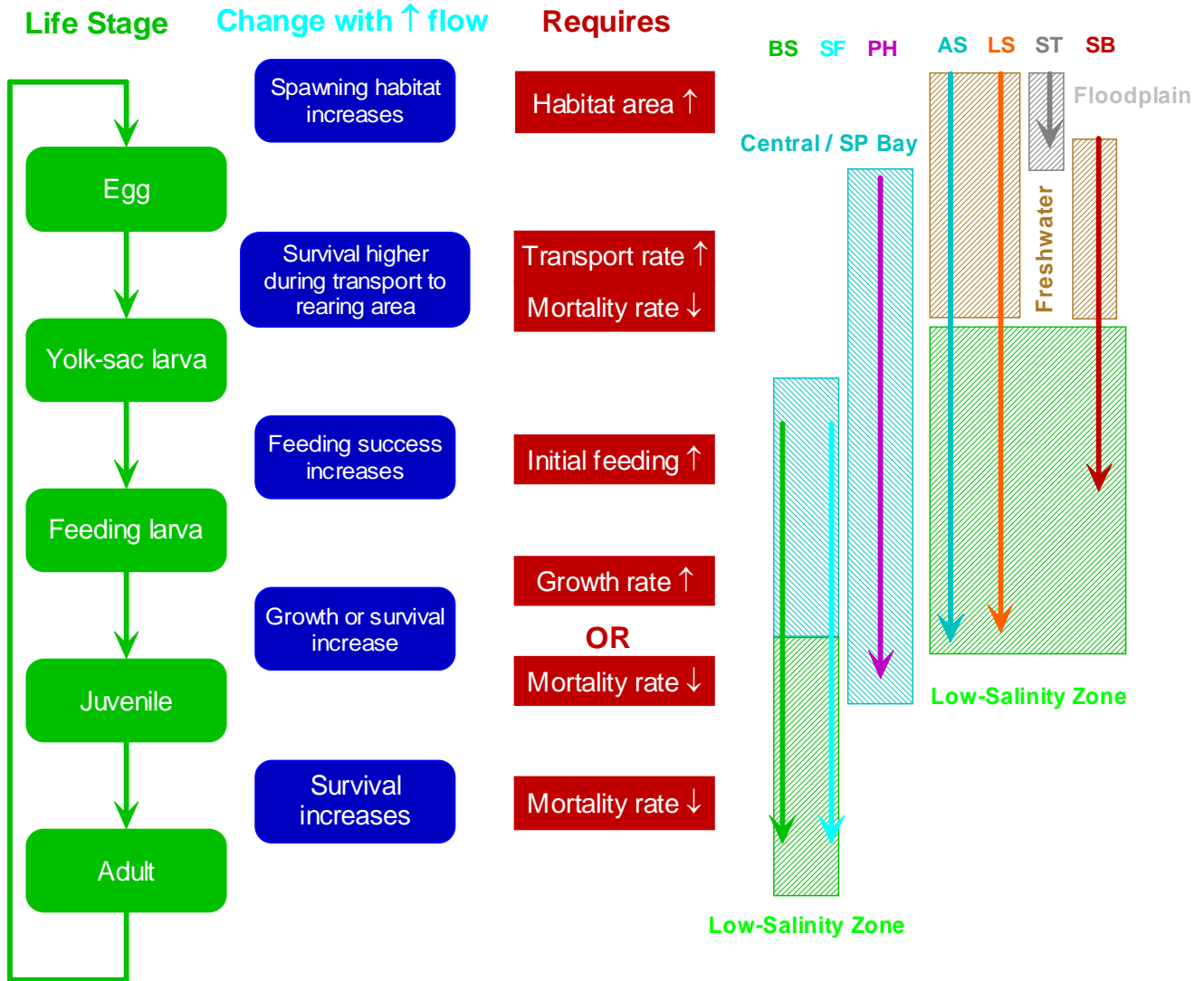
Figure 1
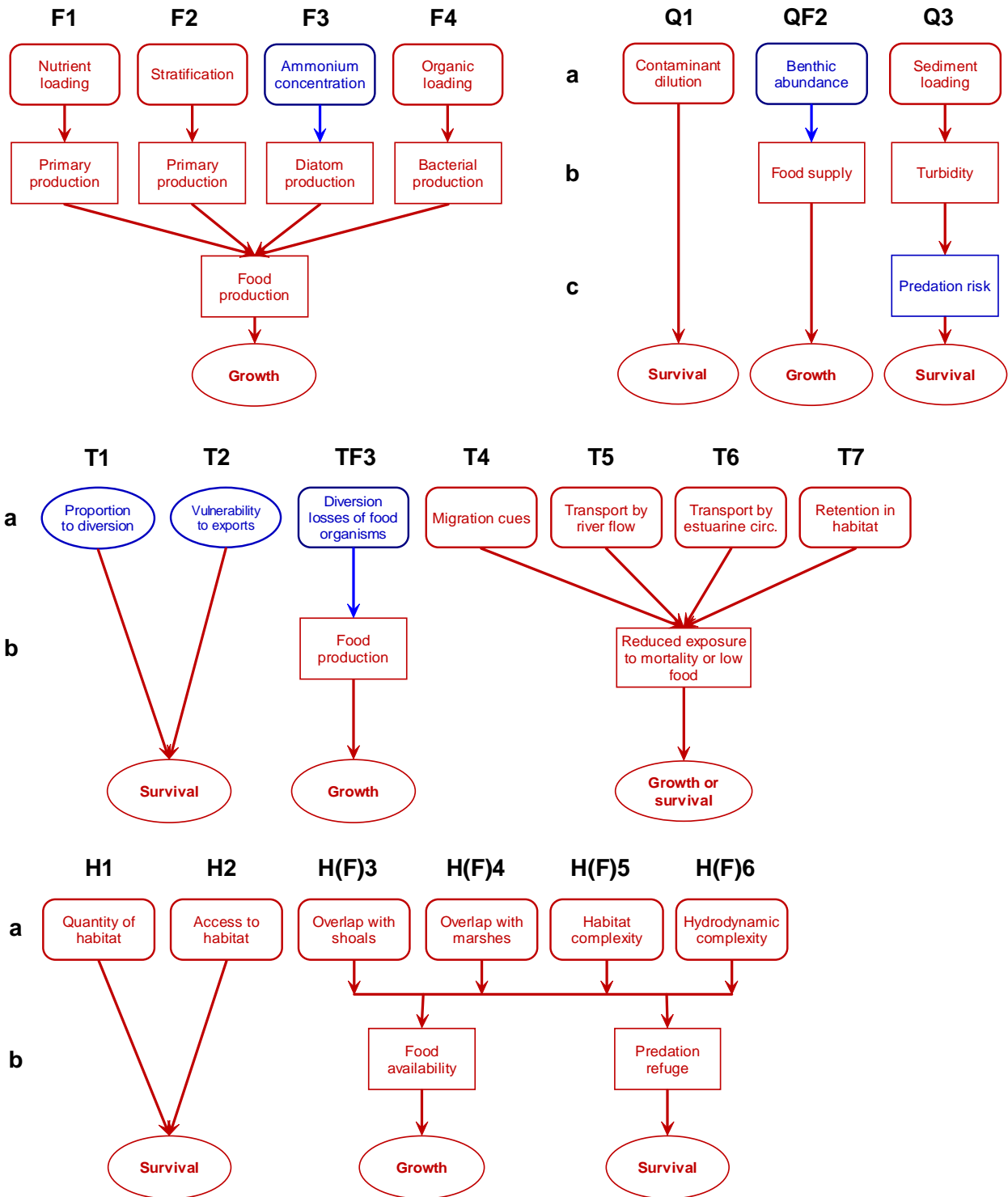
Figure 2

Figure 3

Figure 4

Figure 5

Key Study

Field/Lab
Model
Data

Feeding

Early growth
increases

Cohort Analysis

Higher
Growth

YES

Feeding Studies

Habitat

H1: Area increases

Habitat model
(TRIM3D)

Habitat description
from data

Habitat
increases

ND

Habitat analysis

Predation

Q3: Turbidity
reduces predation
rate

Predation Model

Predation
Potential

YES

Predation Studies

Transport

T6a:Transport
faster

PT model
(TRIM3D)

Faster

YES

T6b: Survival lower
during transit

Life table /otoliths
for mortality

HIgher

YES

Figure 6

Field/Lab
Model
Data

Seaward ⋮ Delta

Habitat

Feeding **Water Quality** | **Transport** **Habitat**

| T7: Retention in habitat higher | H1: Area increases | Fnc: Early growth increases | Q3: Turbidity reduces predation rate | T5b: Survival increases | H1: Spawning area increases |

| PT Model | Habitat model (TRIM3D) | Habitat description from data | Otolith Studies | Predation Model | Otolith Studies | Determine spawning area |

| HIgher | Habitat increases | Higher Growth | Predation Potential | | Habitat increases |

ND* | YES | YES | | YES

| Predation Studies | Habitat analysis | Feeding Studies | Predation Studies | | Habitat analysis |

Figure 7

LSZ

Feeding

Fnc: Early growth increases

Otolith Studies

Higher Growth

YES

Feeding Studies

Predation

Q3: Turbidity reduces predation rate

Predation Model

Predation Potential

YES

Predation Studies

Habitat

H1: Area increases

Habitat model (TRIM3D)

Habitat description from data

Habitat increases

Yes

Habitat analysis

Rivers/Delta

Transport

T5b: Survival increases

T5b: Mortality higher in river

T5b: San Joaquin input increases

Egg and Larval Studies: Analyze data, Samples?

Field Sampling for Mortality

Otolith Studies

Field/Lab
Model
Data

Key Study?

Figure 8

Appendix A. Predator-Prey Model

We developed a simple model based on that of Aksnes and Utne (1997) to explore the relationship between turbidity and the relative growth and survival probability of a generic planktivorous fish species in the presence of a piscivore. The model is one-dimensional (vertical) with no temporal variability. The outputs are growth rate and mortality risk for the planktivore under as a function of depth, under different conditions of turbidity and light level. We used available data for abundance of plankton, planktivores, and piscivores, assuming a constant size in each category. We used bioenergetic models to estimate maximum feeding rate and a simple foraging model based on visual perception to estimate actual feeding rate.

Chief assumptions of the model are:
- Constant abundance of planktivores and piscivores in time and in the vertical dimension
- Constant swimming speed for both planktivore and piscivore
- Encounter rate between planktivore and piscivore is random, governed by the swimming speed of the piscivore only
- All predation is visual with acuity affected only by light and turbidity
- Maximum consumption rates of planktivore and piscivore are determined by bioenergetics

The feeding rates of both fishes were modeled using the same approach with different parameters for each. Both are assumed to feed only visually. The description below is general and applies to both fish; subscripts are added later for zooplankton (z), planktivorous fish (f), and piscivorous fish (p).

Feeding rate is linearly related to food abundance (concentration) under the assumption that handling time of prey is negligible. The maximum feeding rate is determined by applying the Wisconsin bioenergetic model using parameters in Table B1. Feeding rate is based on a constant swimming speed, with a search area that depends on reactive distance, a function of turbidity and light. Fish and plankton are assumed to be randomly distributed in the environment.

The feeding rate of a predator is based on the encounter rate between predator and prey:

$$F = (1 - P_e)\, ER = (1 - P_e)\, \pi\, (r \sin \theta)^2\, v\, N \tag{1}$$

where symbols are as in Table B1. The maximum feeding rate is the maximum daily ration, C_{max}, calculated using the Wisconsin bioenergetics model. The swimming speed v is assumed to be constant for the piscivore, but for the planktivore we assume that the more frequent the encounters with the predator the less time they can spend swimming and feeding. We represent this as

$$v = v_0\, e^{-ER\, b} \tag{2}$$

where ER is the encounter rate between piscivore and planktivore, and b is a constant.

The visual range *r* is assumed to be the same as the reactive distance, and is determined as (Aksnes and Utne 1997):

$$r^2 e^{cr} = A_p C_0 E' \frac{I}{I + K_e}$$
(3)

This equation relates the visual distance r to the beam attenuation c as well as to the available light E_b. The combined parameters $A_P C_0 E'$ were estimated as T_1 by Aksnes and Utne (1997), but since this includes the cross-sectional area of the prey (as seen by the predator) we calculated $T_2 = C_0 E'$ from their results, leaving area A_P as a parameter that depends on prey length:

$$A_P = 0.1 L^2$$
(4)

as used in Aksnes and Utne (1997). For conversion of various measures of turbidity, we used:

$$c = 3 k$$
(5)

from Kirk (1984), where k is the diffuse attenuation coefficient, which was related to Secchi depth by a regression using 4639 data points from the IEP water quality monitoring program:

$$k = 0.36 + (0.60 \pm 0.01) / \text{secchi},$$
(6)

where the error bounds are 95% confidence limits, and the standard deviation of residuals was 0.47 m^{-1}. To obtain experimental parameters from literature data, we developed a relationship between k and turbidity in nephelometric turbidity units (NTU), which depends on characteristics of the particulate matter. Data for this were also from IEP monitoring:

$$k = 0.53 + (0.49 \pm 0.002) \text{ NTU}$$
(7)

Light levels in experimental work are typically reported in Lux. For sunlight 1 lux = 0.0185 μE m^{-2} s^{-1}. To apply these results to the field data, we fitted inverse Secchi depth (linearly related to k, above, and with a better error distribution than Secchi depth) to X2 and a locally-weighted smooth function of log salinity, using a generalized additive model (Splus 6.2, Venables and Ripley 2002). This model was then used to determine Secchi depth under selected conditions of flow and salinity.

Two parameters specific to the characteristics of predators were estimated by fitting equation 3 for reactive distance approximately to data from Mazur and Beauchamp (2003, their Figure 1). The parameter T_2 is a scaling parameter that sets the reactive distance for maximum light at a given beam attenuation coefficient.

To set up the model, parameters were first selected including surface irradiance, diffuse attenuation coefficient, and abundance values. Generally the remaining parameters were left

alone once reasonable values had been established. Using irradiance at 1-meter depth intervals, the visual ranges of planktivores and piscivores were calculated using equation 3. Then these values were used to estimate encounter rates of planktivores with piscivores using equation 1, which in turn were used to alter the swimming speeds of planktivores. Then feeding rates of each were calculated, and for the planktivores these were converted to growth rates and mortality rates, taken here to represent a risk to the planktivore.

Results

The model fit to the secchi disk data from the DFG zooplankton survey (Figure A1) shows that Secchi depths averaged about 0.2 m in the LSZ at high flow, grading to 0.6 m at low flow and far from the LSZ, either seaward or landward. This is a 3-fold change in water clarity, which could substantially affect predation rates, particularly through light attenuation in deeper water. Note, however, that actual secchi depths vary substantially around these modeled values (Figure A2).

Using a mid-range secchi depth of 0.36m gives a value for k of 2 m^{-1}, which implies that light attenuation is sufficient to eliminate visual predation below about 8m depth. This is shown by the graphs of reactive distance for planktivore and piscivore (Figure A3), which decay sharply from their near-surface maxima below about 2m depth, as light begins to decrease below the point at which it limits prey perception.

The implications of this encounter rate for consumption rate of the piscivore and planktivore are that at all depths the piscivore has a higher specific feeding rate (Figure A4). For both fish this rate is limited in the upper 3-5m of the water column by bioenergetics, whereas below that it is limited by light.

The growth rate of the planktivore exceeds the predation mortality rate only in a narrow range of depth; above about 4m depth the predation rate (equivalent to a predation risk) greatly exceeds the growth rate (Figure 4). Explorations of the parameter space did not reveal any striking variations in the model's outcome. In particular, no combination of parameters led to a situation in which planktivores did well in turbid water; the best they could do is less poorly.

One of the functions of modeling is to reveal the outcomes of strings of assumptions about nature, and then to expose those outcomes to comparison with what we know about how the ecosystem works. One thing we are reasonably sure of is that both planktivores and piscivores inhabit all parts of the water column in the LSZ. This is at odds with the predictions of our model; therefore something must be wrong with our model. Thus these results fail to support the putative mechanism described above. This is not to say that the mechanism does not work as stated. Rather, some features of the model output are at odds with observations. Therefore the model is inadequate to represent the predator-prey interaction in a sufficient way to allow inferences to be made about the role of turbidity.

The result of the model that is most surprising is that it shows very little scope for growth and success of planktivores. One way this result could be overturned is if schooling behavior were to be modeled. Fishes are believed to school at least partly to reduce predation risk. Therefore including schooling behavior might reduce the modeled predation risk and also provide more

realistic estimates of the influence of turbidity. Schooling behavior can be investigated only using an individual-based model.

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Table A1. Summary of parameters used in the model, with values and sources of information.

Symbol	Description	Units	Piscivore	Planktivore	Plankton	Source
N	Abundance	m^{-3}	0.001	0.01	1000-10000	Field data (exc. Piscivore)
I_0	Subsurface Irradiance	$\mu E\ m^{-2}s^{-1}$	Assumed 50% surface = max 700			U.C.Davis
k	Diffuse attenuation coefficient	m^{-1}	Determined from Secchi depth			IEP data: Secchi depth, k, turbidity
P_e	Probability of escaping attack	–	▓	0.5	0	Assumption
L	Length	m	0.2	0.05	0.001	Assumption
C_0	Inherent contrast of prey	--	See T_2 below			
E'	Sensitivity parameter to contrast	--				
T_2	Product of previous 2 parameters	–	4500	11.6×10^{-9}	▓	Literature; see text
K_e	Saturation parameter	$\mu E\ m^{-2}s^{-1}$	0.1	4	▓	Literature; see text
v_0	Swimming speed without predators	$m\ s^{-1}$	0.2	0.05	▓	1 body length/sec
b	Relates swimming speed to predation risk	s^{-1}	▓	0.07	▓	Assumed: speed reduced by half at 10 encounters/hour
Cmax	Maximum daily consumption	$gC\ d^{-1}$	1.4	0.05	▓	From bioenergetics model
ER	Encounter rate	s^{-1}	Calculated			
r	Visual range	m	Calculated			
v	Swimming speed	$m\ s^{-1}$	Calculated		▓	From v_0 and b
c	Beam attenuation coefficient	m^{-1}	Calculated			c = 3 k
A_P	Area of prey	m^2	▓	Calculated		$A_P = 0.1\ L^2$
I	Irradiance	$\mu E\ m^{-2}s^{-1}$	$I_0\ e^{-kz}$			Variable with depth and attenuation
F	Feeding rate	s^{-1}	Calculated			From encounter rate max=Cmax
W	Mass of the fish	gC	15	0.2	10^{-5}	

Figure A1   Secchi depth fit to a smoothed curve and interpolated at selected points of salinity and X2. Data from the IEP zooplankton survey.

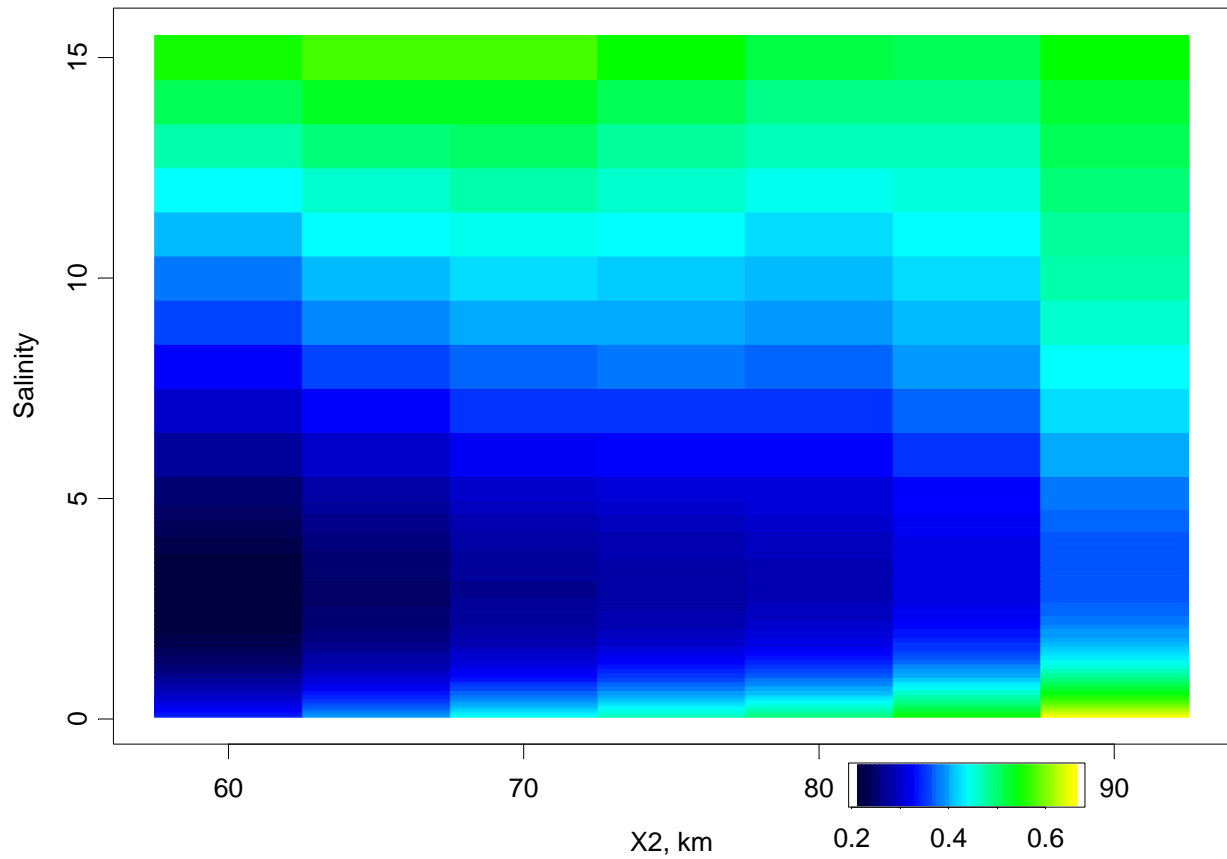Secchi Depth: model fit to zooplankton survey data

Figure A2   Secchi depth within the salinity range of 1-6 plotted against X2 on the day of each sample. Data from IEP zooplankton, water quality, 20mm, summer townet, and fall midwater trawl surveys.
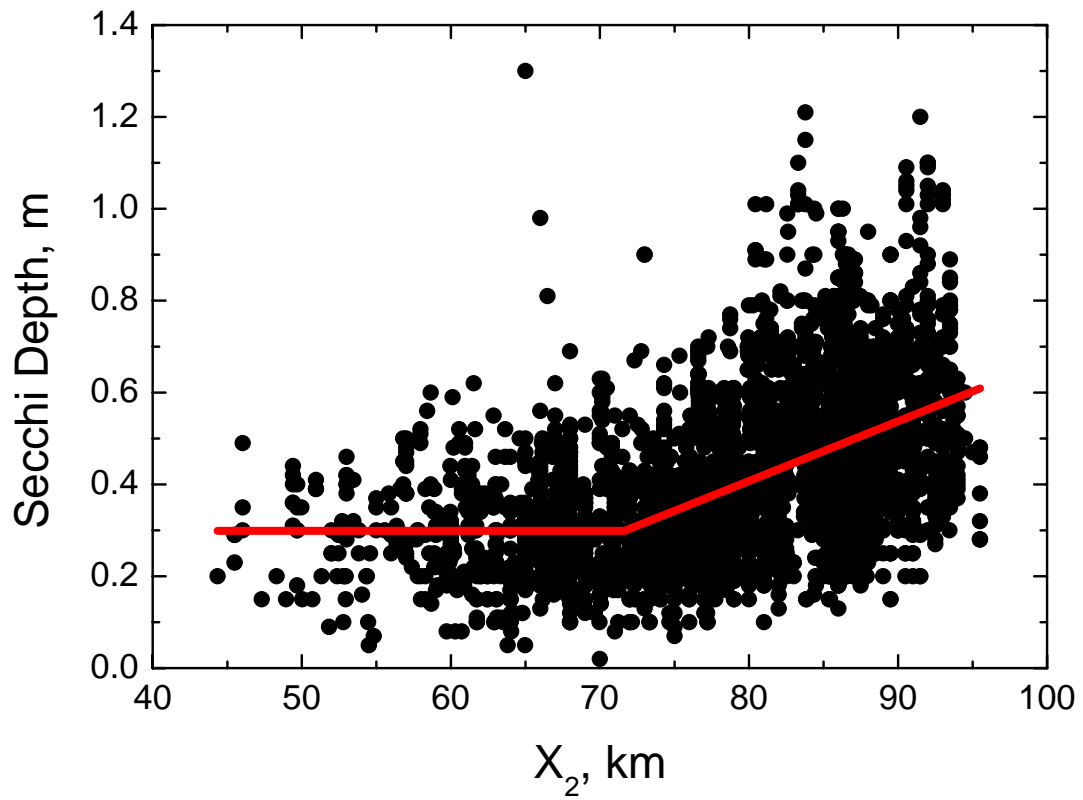
Figure A3. Reactive distances of piscivore and planktivore as a function of depth in the water column. Model output using parameters in Table A1.
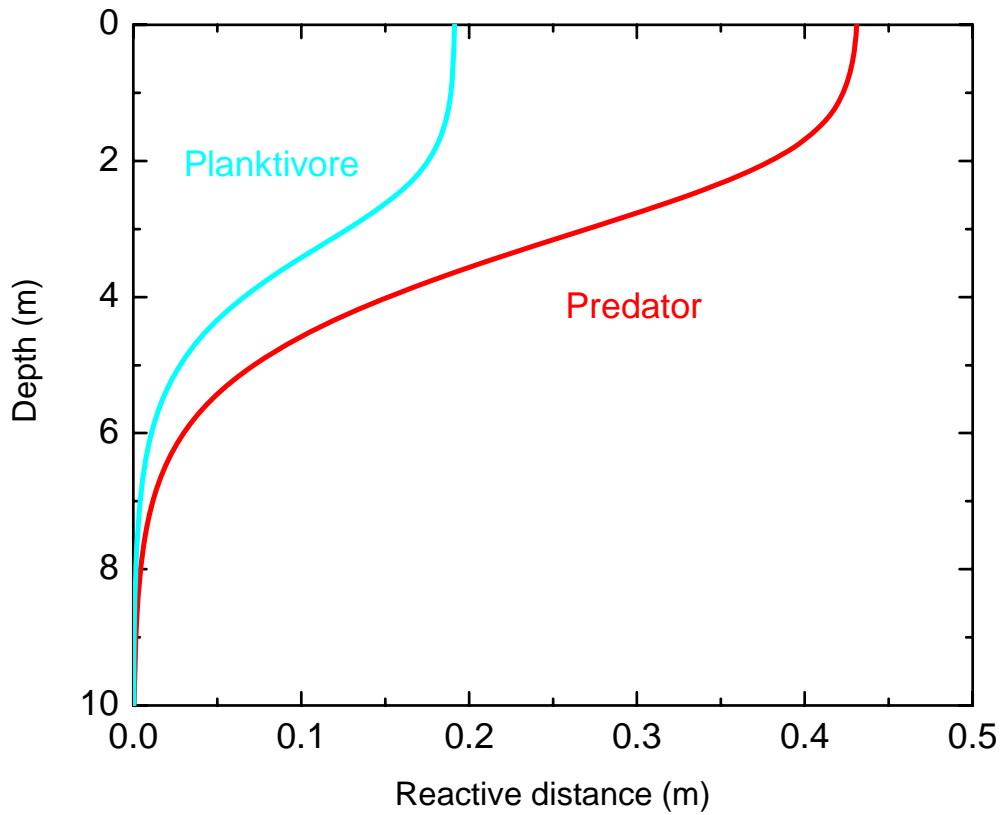
Figure A4. Daily specific growth rate and mortality risk of planktivore as a function of depth in the water column. Model output using parameters in Table 1.
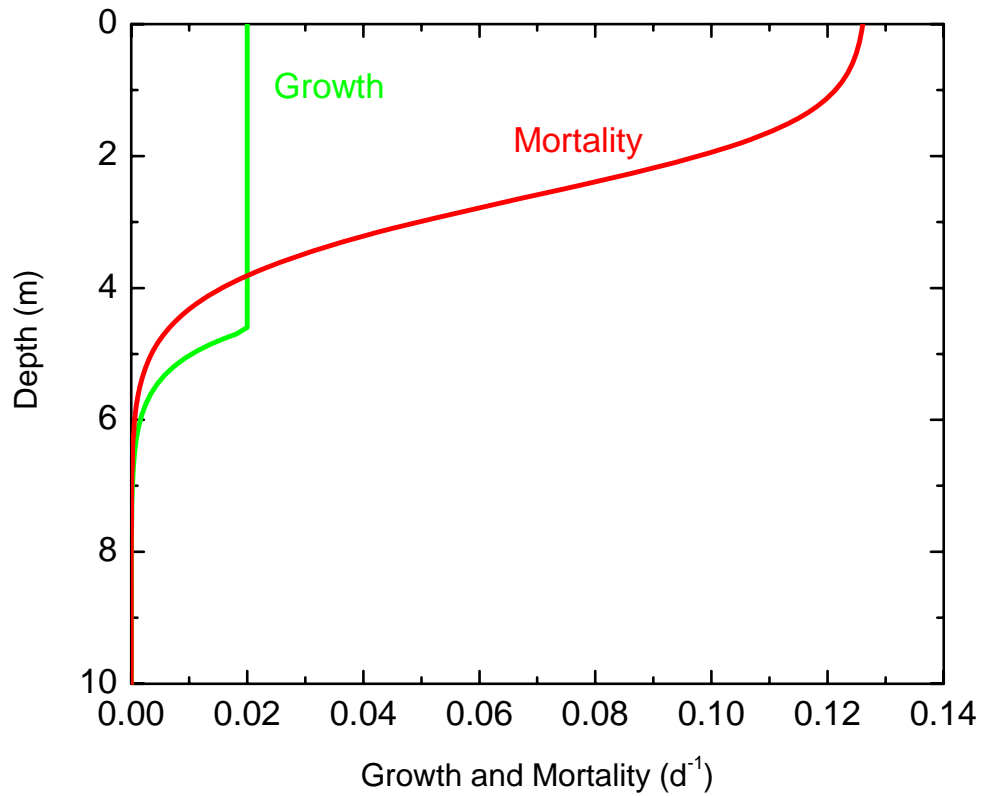
Appendix B
Manuscript in Preparation:

Variation of physical habitat for estuarine fish with freshwater flow

Kimmerer, W.J.
Gross, E.S.
MacWilliams, M.L.

Variation of physical habitat for estuarine fish with freshwater flow

Kimmerer, W.J.
Gross, E.S.
MacWilliams, M.L.

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Abstract

We estimated how the quantity of physical habitat for several fish and one shrimp species varies with freshwater flow in the San Francisco Estuary. Data from 5 data sets from 4 sampling programs were used to determine resource selection functions. We applied generalized additive models (GAMs) with salinity and depth as predictors to determine separate functions for catch per trawl and frequency of occurrence, and used bootstrap resampling to assess the reliability of the end results. Depth was a useful predictor only for one data set in which an otter trawl was used to collect the organisms, so only salinity was used for the other 4 data sets. A calibrated hydrodynamic model, TRIM3D, was run for 5 steady freshwater flow scenarios to produce tables of area of the estuary by salinity and depth. The GAM curves were used as weighting factors, multiplied by the volume in each salinity and depth range to determine an index of total habitat in the estuary for each flow scenario. The relationship of these habitat indices to an index of freshwater flow were compared with similar relationships for abundance indices. In only two cases were the slopes of these relationships consistent, implying that for most species the extent of physical habitat is not the most important mechanism underlying responses of abundance to freshwater flow.

Introduction

Variability in freshwater flow provides the principal mode of interannual and seasonal variation of conditions in many estuaries (Skreslet 1986). River discharge into estuaries may be sensitive to climate change (Scavia et al. 2002) and may be substantially altered by both climate change and human demand (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 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 abundance or harvest of benthic invertebrates (Aleem 1972, Gammelsrød 1992, Montagna and Kalke 1992, Wilber 1992, 1994) 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). According to one proposed mechanism (Mechanism #10, Kimmerer 2002b), increasing freshwater flow increases the area or volume of physical habitat for biota. This mechanism has been proposed to explain how abundance of Sacramento splittail, *Pogonichthys macrolepidotus,* increases with freshwater flow in the upper San Francisco Estuary (Sommer et al. 1997). High flow inundates floodplains adjacent to the estuary, and splittail gain access to large areas of foraging, spawning, and rearing habitat. Chinook salmon may also benefit from inundated floodplains through increased foraging opportunities (Sommer et al. 2005). However, for species for which the floodplain is not an important habitat, there is little evidence for or against this mechanism.

In this paper we examine two characteristics of physical habitat for a variety of fish and one shrimp species: salinity and water depth. The objective was to determine how habitat so defined varies with freshwater flow, and the extent to which these habitat responses translate to flow responses. Salinity is clearly a key attribute of the habitat of estuarine species (Kimmerer 2004 Figure 35), and water depth is likely important for some, particularly demersal species. Furthermore, the location of isohalines varies with freshwater flow, so that the joint salinity-depth distribution varies with flow. Turbidity is also an important attribute of habitat, and may provide cover for open-water species (Feyrer et al. 2007). 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.

We follow Jassby et al. (1995) and Kimmerer (2002a, b) in using X2, 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 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 fish and shrimp abundance or survival have been related to X2 (Jassby et al. 1995), and these relationships have been amended to account for

declines largely attributed to the effects of grazing by an introduced clam (Kimmerer 2002a). More recently some of the species included in those analyses have suffered further declines (Sommer et al. 2007). We have updated these relationships through 2005-2007, and in this paper we combine hydrodynamic modeling and analysis of abundance and distribution data to ask whether the observed relationships of abundance to X2 could be due to correlated changes in the extent of physical habitat.

*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 2005). 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.

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 time scales (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. 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.

Methods

Data sources

Details of the calculation of X2 and the abundance indices used in determining the abundance-X2 relationships are presented here in abbreviated form (see Jassby et al. 1995, Kimmerer 2002a). Briefly, X2 was initially determined through interpolation of salinity between sampling stations. Since 1992 X2 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 common species were obtained from 5 data sets from 4 sampling programs. All were for young-of-the-year except for starry flounder, which was collected most effectively as age-1 fish. The summer townet program (Turner and Chadwick 1972) took two to five surveys during 1959-2007 (except 1966) at approximately two-week intervals starting in June. Triplicate tows were taken throughout the northern estuary at a median of 27 stations.   The striped bass young-of-the-year (YOY) index was interpolated to the time when the mean size of the young striped bass in the catch was 38mm. The delta smelt index was calculated from the mean abundance in the two surveys used to determine striped bass abundance.

The fall midwater trawl program obtained data during 1967-2007 (except 1974 and 1979), monthly from September to December at a median of 88 stations in the northern estuary (Moyle et al. 1992). The annual midwater trawl 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 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 the fall survey and an otter trawl. 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, but indices are not yet available for 2007.

Data from the above programs were used for both habitat use and for updating the abundance-X2 relationships. Data were also obtained for habitat use only from the spring-summer "20mm survey" program designed to capture late larvae and juveniles of delta smelt (Dege and Brown 2004). Triplicate tows were taken in 8-9 surveys between March -April and July-August during 1995-2006 at a median of 41 stations throughout the northern estuary.

Analyses of relationships to X2 followed previous approaches (Kimmerer 2002a). For most species log of the abundance index was related to X2 averaged over several spring months when each species is likely to be most vulnerable to freshwater flow effects. In contrast to previous analyses we used abundance rather than survival for Pacific herring. For most species we included a step change in 1987-1988 to allow for the possibility of an effect of declining food supply. For delta smelt in the townet survey the slope changed in 1981-1982 so that step was included in the model as an interaction term.

For striped bass two kinds of response variable were used, and the step was in 1995-1996. Abundance indices from each of the sampling programs were truncated to data after 1977 (summer and fall surveys only) because the large decline in egg production in 1976-1977 caused a substantial decline in YOY (Kimmerer et al. 2000). We also used survival from egg to the first summer, calculated as described in Kimmerer (2002) with one modification. Briefly, egg production was calculated from adult abundance by age determined as Petersen estimates from mark-recapture studies, and from age-specific fecundity (Kimmerer et al. 2000). The summer abundance index was the mean catch per trawl in the summer townet survey, which is closely related to the townet index used previously ($r = 0.95$ between annual values for the entire time series). Adult striped bass were sampled only during even years between 1994 and 2002, and abundance estimates are not yet available for 2006-2007. We filled in these values by interpolation (level extrapolation for the last 2 years) for graphs only, but excluded the resulting values from statistical analysis.

Habitat calculations: Generally habitat is defined by use, and use is determined through sampling (Manly et al. 2002). Our general approach was to use sampling data to develop resource selection functions describing habitat use as a function of salinity and depth, and combine those with estimates of the volume in the estuary within each combination of salinity and depth. For a given species:

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

where H is an index of habitat as a function of freshwater flow Q, h is a discrete or continuous resource selection function, based either on catch per trawl or probability of capture as a 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. In this discrete formulation S and Z are divided into blocks of 1 psu for salinity (i.e., 0-1, 1-2, etc.), and 1-m blocks of depth in the top 20m and 5-m blocks below 20m.

The index H is taken as proportional to the sums on the right of equation 1 because the function of habitat use h has an arbitrary scaling factor (Manly et al. 2002). Although habitat use can be expressed in terms of probability of capture, this probability still depends on the particular gear used in relation to the species being captured, and absence from the sample does not imply absence from the habitat. Thus, presence or absence in a sample depends on detection limits and is not a fundamental attribute of the distribution of the population being sampled.

We calculated functions h as described below for common species using raw catch data from the four sampling programs described above. For common species in each of the five survey/gear combinations, 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 each species was abundant; this was unnecessary for the other surveys because of their more limited durations. We did not include Sacramento splittail in this analysis since its spawning and rearing habitat is outside the domain of the hydrodynamic model used to determine $V_{S, Z}$. For the same reason other abundant species (e.g., threadfin shad, *Dorosoma petenense*) that are found almost entirely in freshwater were also excluded.

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). Following Swartman et al. (1992), Maravelias (1999), Stoner et al. (2001), and Feyrer et al. (2007), we used generalized additive models (GAMs) to fit data on both catch per trawl and frequency of occurrence to salinity and (in some cases) depth. 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 can also have non-normal error distributions. We used a locally-weighted regression (loess) as the smoother (Swartzman et al. 1992) for salinity, and where depth was included used a linear fit, and applied a binomial error distribution to frequency of occurrence and a Poisson error distribution to catch per trawl. 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.

We determined the GAM functions for both catch per trawl and frequency of occurrence for each species/sampling program combination. As shown below, the outcomes (H in Eq. 1) were usually similar for these two approaches, but the actual habitat curves (h in Eq. 1) were often

quite different, with the frequency of occurrence resulting in broader distributions of habitat than the catch per trawl.

Exploratory analyses were used to determine the best span parameter for the loess fits, and to examine the importance of water depth as a predictor variable. Because of the large number of data points in each analysis, 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 determined as

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

where D_{res} is residual deviance and D_{tot} is total deviance. 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. However, only the Bay Study sampling covered most of the joint range of depth and salinity. Because of their more limited geographic range, the other surveys had relatively few deep stations and relatively poor coverage at high salinity. Therefore depth was included for all species included in the Bay Study otter trawl data but for none others.

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

Model calculations 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 3-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 m by 200 m by 1 m deep cells. Because the bathymetric variability (geometry) 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 has been 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 validated using data from the dry period in 1994 (Gross et al. in prep.). Modeled salinity was correlated with data from 14 continuous monitoring sensors with correlation coefficients of 0.9 to 0.99, and mean errors in salinity up to 1.8 psu at the bottom sensor in central Suisun Bay.

The model was run in a steady-state mode using a repeating daily tide comprising the M2 component modified to a 12-hour period and the K1 component. Freshwater flow from the Delta was also steady in each simulation at one of 5 flow values. For consistency with the X2-abundance analyses, X2 values corresponding to each flow level were calculated using a steady-state version of the daily time-series equation in Jassby et al. (1995). The model was run to steady state before habitat calculations were made.

For each flow value and each estuarine basin, daily mean salinity was calculated for each grid cell. These values were averaged over the water column except that 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 1-psu increment and total water column depth below the NGVD datum (roughly mean sea level) within each 1- or 5-meter depth increment. The portion of the Delta not resolved by the model was assumed to have a constant depth of 6m and to be entirely freshwater.

The habitat quantity H was calculated for each species/sampling program combination, and for each flow scenario, using the calculated GAM function h, and the 25 bootstrapped values of h were used to determine sample estimates of H. These were then used to calculate statistics for regressions of log H on X2, which were compared with the slopes of abundance vs. X2 to determine whether these slopes were similar enough to the habitat slopes to suggest that habitat variability could underlie the relationships of abundance to X2.

We repeated the calculations of H for the mean GAM functions using bottom salinity instead of the water-column mean, except for the Bay Study otter trawl data which had been calculated with bottom salinity. Correlations between H values determined with bottom salinity and those determined by water-column means were all > 0.94 and most were > 0.99. The remainder of the analyses of these data were conducted using the water-column means.

Results

The X2 relationships (Fig. 2, Table 2) are not markedly different from those previously published, except that the slope of the X2 relationships of abundance (as opposed to egg-young survival) index of Pacific herring was essentially zero. Species for which data were available from more than one survey showed consistent patterns in all of the surveys, except for delta smelt: smelt captured in the summer townet survey had a change in slope after 1981 (Fig. 2) whereas smelt captured in the midwater trawl survey had a step change in 1987-1988 and essentially zero slope with X2. Other species not included in the previous analyses had no significant X2 relationships (Table 2).

Fits of the GAM models 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 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. 3) Excluding depth from the analysis 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 (Table 3).

Habitat curves generally fit the data better with a shorter span parameter, but at the expense of excessive small-scale fluctuation (Fig. 3, for salinity only). For some species the habitat curves based on catch per trawl gave tighter responses to salinity than did those from frequency of occurrence (e.g., Fig. 3 A, C, Fig. 4). This occurred because high frequencies of occurrence could be associated with both high and moderate catch per trawl. Simulations based on assumed underlying distributions with respect to salinity (not shown) confirmed that habitat curves based on catch per trawl were usually closer to the underlying distribution than those based on frequency of occurrence, which tended to have fat tails.

Bootstrap replicates generally had similar shapes to the calculated habitat curves, and variable peak values (Fig. 4). Differences were more pronounced with the catch per trawl than 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 X2.

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

Output of the TRIM model (Fig. 6) showed progressively seaward movement of the salt field with increasing Delta outflow (Fig. 7). In addition, the strength and extent of predicted 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 shows the interaction of salinity with bathymetry and how this varies with flow (Fig. 8). 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 region of salinity between 5 and 10 psu increased markedly because of the freshening of deep areas in Carquinez Strait and then inundation of extensive shallow areas of San Pablo Bay (Fig. 6). 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. Nevertheless, because of their size these regions contributed to a substantial increase in volume between 20 and 30 psu as flow increased, at the expense of salinity >30 psu.

Several examples show the relationships of habitat quantity to X2 (Fig. 9; see Table 1). In most cases the slopes had very small confidence limits (i.e., the bootstrap samples were close together). The habitat-X2 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. 10). Habitat-X2 relationships based on catch per trawl were similar to those based on frequency of occurrence.

Slopes of the abundance-X2 relationships were consistent with habitat-X2 relationships in only a few cases (Fig. 10). Bay shrimp and starry flounder showed no response of habitat volume to flow, whereas abundance indices of both were moderately related to flow. Pacific herring and northern anchovy had essentially zero slopes based on catch per trawl, and generally small slopes based on habitat.

American shad and striped bass had significant negative slopes in the abundance relationships and similar negative slopes from the habitat relaionships (Fig. 9). Longfin smelt had the strongest negative slope from the abundance relationships and weak but still negative habitat slopes. Habitat relationships of delta smelt and striped bass had more negative slopes in the earlier surveys, probably because the salinity distributions of the earlier life stages occupy areas that are fresher and therefore more responsive to changing flow than the more brackish regions (Fig. 8).

Discussion

Habitat is a readily accessible concept for terrestrial and nearshore aquatic systems. For example, 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 .

Two fundamental approaches can be used for determining habitat quality. First, laboratory or field observations of physiological or behavioral response to a selection of habitat variables can be used to construct habitat suitability indices, which are then applied to the field. This has the disadvantage of requiring substantial investment in experimental work that grows geometrically as the number of alternative attributes increases. It is also highly unsuitable to open-water species because of their large individual ranges. Second, field observations can be made of abundance or presence of the species in samples. This approach incorporates an underlying assumption that habitat suitability is proportional to observed distribution, which is unlikely to be true because of unobserved biotic interactions or habitat attributes not included in the model. Nevertheless, this is really the only approach available for open-water species.

Several approaches have been proposed for determining the extent of habitat based on field surveys, notably the use of resource selection functions (Manly et al. 2002). These functions describe the probability that members of a population will use a particular resource unit, which in the context of this study could be a unit of habitat. These functions can be based on presence vs. 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.

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 relatively 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 estuarine nekton populations means that some individuals are likely to be found in a wide variety of habitat characteristics (e.g., see Figure 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).

Additional attributes of habitat might have added explanatory power to our analysis. Turbidity is an important habitat descriptor for some species and life stages (Feyrer et al. 2007). Turbidity in the San Francisco Estuary is principally due to suspended sediment concentrations, which are highly variable but respond only weakly to freshwater flow (Schoellhamer 2002). Secchi depth was also weakly responsive to 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 the patterns did not change notably. Thus, while our description of habitat is clearly over-simplistic, the strong spatial response of salinity to flow ensures that our model captures most of the flow-related variability.

Of the species we examined, only American shad and striped bass had abundance (or survival) relationships to X2 that appeared consistent with their relationships of habitat to X2 (Fig. 10). Although this finding does not rule out other mechanisms, it provides some support for the idea that increasing quantity of habitat as defined by salinity could explain the X2 relationships of these species.

Confidence limits for relationships of abundance with X2 for longfin smelt, bay shrimp, and starry flounder did not overlap with those of any of the corresponding habitat 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, 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, then spread rather widely throughout the northern estuary (Rosenfield and Baxter 2007). Abundance of longfin smelt varied by about 2 orders of magnitude over the range of X2 values, although abundance declined substantially in 1987-88 and again in 2007 (Fig. 2). The modest slope of habitat to X2 would allow for only about a 2-fold increase over that X2 range. Furthermore, the extent of the longfin smelt population in terms of distance up the axis of the estuary does not increase with increasing flow (Fig. 10 in Kimmerer 2002b).   Therefore the mechanism underlying the X2 relationship for longfin smelt remains unknown, but it may be related to the shift toward greater depth at higher salinity, possibly implying a retention mechanism.

Habitat for northern anchovy was negatively related to X2 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 survey is therefore more applicable to northern anchovy than is the fall midwater trawl, and it gave a zero slope for habitat vs. X2 as did the abundance index.

Physical habitat of delta smelt and striped bass not only responded similarly to flow conditions but the habitat selection functions for each sampling program were similar between the two species (Fig. 10). 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 X2 relationships whereas abundance of delta smelt did not. Most delta smelt live 1 year, resulting in less autocorrelation due to stock size. Adding the previous year's fall midwater trawl index did not improve the fit of the X2 model. Despite the evident increase in the amount of habitat, delta smelt abundance appears to be regulated by other factors so far unidentified.

In summary, for only two species does physical habitat respond to flow similarly to abundance. We have considered only two attributes of habitat, and at the very least would prefer to include secchi depth (or another measure of turbidity) in the models (Feyrer et al. 2007). 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, alternative explanations to habitat must be invoked for the observed relationships of most of the estuarine-dependent nekton species to freshwater flow.

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Table 1. Species included in the abundance-X2 or habitat analyses. Life history information includes months of higher abundance used in analyses with Bay Study data. Source columns give the number of samples for each survey and each species; these are reduced from the maximum for the Bay Study samples because of the retricted time period included in the analysis.

Taxon	Abbrev.	Life History Information	Source				
			20mm	TNS	MWT	Bay MWT	Bay OT
Bay shrimp *Crangon franciscorum*	BS	Adults reproduce in coastal ocean, young move into the estuary in spring to rear in shallow areas (Hatfield 1985). May – November.					6518
Starry flounder *Platichthys stellatus*	SF	Adults spawn in winter, larvae and juveniles move far into the estuary in spring to rear (Emmett et al. 1991). All year.					10820
Pacific herring *Clupea pallasi*	PH	Adults migrate from ocean to lower estuary in winter to spawn; larvae rear in estuary (Emmett et al. 1991).	12887				
Northern anchovy *Engraulis mordax*	NA	Coastal population also resident in estuary (Kimmerer 2006). April - November	12887	6452	13697	8065	
American shad *Alosa sapidissima*	AS	Anadromous, adults spawn in spring, larvae and juveniles rear in estuary (Emmett et al. 1991). May - November			13697	4856	
Delta smelt *Hypomesus transpacificus*	DS	Adults spawn in late winter-spring, larvae and juveniles rear near Low-Salinity Zone (Bennett 2005).	12887	6452	13697		

				Source				
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). May - December	12887	6452	13697	7777	4557
Sacramento splittail *Pogonichthys macrolepidotus*	SS	Adults spawn in early spring on flood plains. Juveniles rear in fresh to brackish water (Sommer et al. 1997).					
Striped bass *Morone saxatilis*	SB	Adults spawn in rivers in spring, larvae and juveniles rear in Low-Salinity Zone (Turner and Chadwick 1972). (May-Dec)	12887	6452	13697	7777	7225

Table 2. Summary statistics for X2 relationships based on species and sampling programs represented in Figure xx (bold), the same species from other sampling programs, and other common species. Sources of the data are: TNS, summer townet survey; M, 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 X2, 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 X2 value and a step change in 1981-1982 (Kimmerer 2002). The fit to striped bass survival (indicated by an asterisk) and abundance indices had step change in 1995-1996, and data before 1978 were excluded (see text). Values presented here are X2 slopes for the individual time periods.

Species	Source	N	p	Intercept	X2	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*	
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
Delta smelt	TNS	20	0.018	-0.3	*0.022 ± 0.017*	
Delta smelt	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	
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	M	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
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	
Northern anchovy	Bay MW	26	0.8	3.8	-0.001 ± 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 | NS |

Table 3. Approximate coefficients of determination based on deviance for 3 alternative models each for abundance and frequency of occurrence, for each species and survey. Alternative models were GAM models 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. Species abbreviations as in Table 1.

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	20mm	35%	38%	37%	29%	30%	30%
NA	20mm	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%
AS	MWT	13%	13%	17%	3%	3%	7%
AS	Bay MWT	37%	39%	43%	16%	17%	19%
LS	TNS	8%	9%	13%	4%	4%	8%
LS	MWT	10%	10%	25%	9%	9%	21%
LS	20mm	21%	21%	32%	17%	18%	26%
LS	Bay MWT	23%	25%	27%	19%	19%	23%
LS	Bay OT	19%	19%	21%	14%	15%	18%
DS	20mm	20%	20%	35%	11%	12%	22%
DS	TNS	13%	13%	18%	16%	17%	19%
DS	MWT	3%	4%	6%	2%	4%	3%
SB	20mm	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%

Figure Legends

9. Map of the San Francisco Estuary showing major basins and the 10m depth contour. Lines with pairs of letters indicate cross-sections shown in model output of salinity profiles (Fig. 7). GG, Golden Gate Bridge; AI, Angel Island; RI, Richmond Bridge; CQ, Carquinez Bridge; MZ Martinez; CH, Chipps Island; CO, Collinsville; EM, Emmaton, and RV, Rio Vista.

10. Log_{10} abundance indices for fish and shrimp (survival index for striped bass) plotted against X_2 as in Kimmerer (2002; Figure 8). Triangles and solid lines, data up to 1987; circles and dotted lines, 1988-2006; filled circles, 2000-2006 (bay shrimp only through 2005). Gray symbols are transitional POD years 2000-2001. Lines are provided only when statistically significant. Regression statistics in Table 2.

11. Example fits of GAM curves to salinity data showing the effect of alternative values of the span parameter on the quality of the fit. Data from the fall midwater trawl survey. Solid line, span=0.5; dashed line, span = 0.25; thin line, span = 0.1. A and C, Delta smelt. B and D, Northern Anchovy. A and B, Abundance data (note scale changes). C and D, frequency of occurrence, with individual data points moved by a small random amount to make them more visible.

12. Example fits of GAM curves to salinity data (heavy lines) with curves derived from bootstrap resampling (thin lines, N = 25). Data from the fall midwater trawl survey. A and C, Longfin smelt. B and D, Striped bass. A and B, Abundance data (note scale changes). C and D, frequency of occurrence, with individual data points moved as in Figure 3.

13. Examples of habitat index H derived from bootstrap resampling. Species and data sources as in Figure 4.

14. Domain and grid of the TRIM3D model showing bathymetry, locations discussed in the text, and a line up the axis of the northern estuary showing km from the mouth of the estuary.

15. TRIM3D model output. Tidally-averaged salinity (psu) along the centerline transect from Golden Gate to Rio Vista (locations identified by heavy lines in Figure 1) for net delta outflows of (top to bottom) 110, 630, and 2810 m^3 s^{-1}.

16. Image plots showing the volume by depth and salinity for each of 5 scenarios of Delta outflow (m^3 s^{-1}). Salinity in increments of 1, depth in increments of 1 m to 20 m, then 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

17. Comparison of slopes of X2 relationships determined using sampling data (filled symbols, from Table 2) with equivalent slopes of habitat indices determined by Eq.1 using TRIM model output combined with distributions of species in terms of habitat. The model results used either catch per trawl (half-filled symbols) or frequency of occurrence (open symbols). Shapes of symbols indicate sampling programs. Error bars are 95% confidence limits; where not shown the error bars are contained within the symbols. Abbreviations for species as in Table 1. The value for the X2 relationship for delta smelt from the townet survey (TNS) includes symbols for data before 1982 and for 1982 and after. That for striped bass includes a symbol for survival from egg to young-of-the year (left) and the young-of-the-year index itself (right).
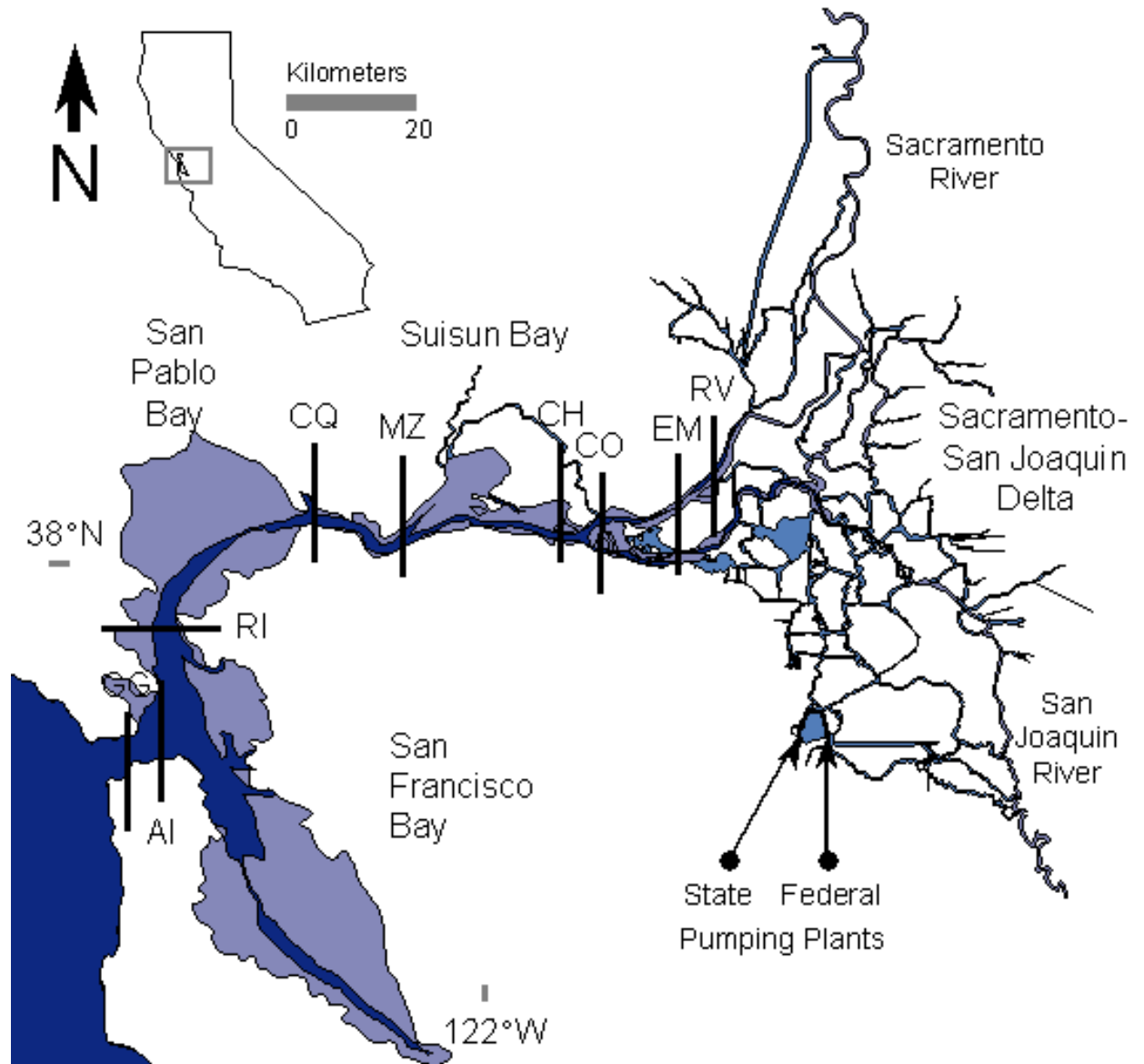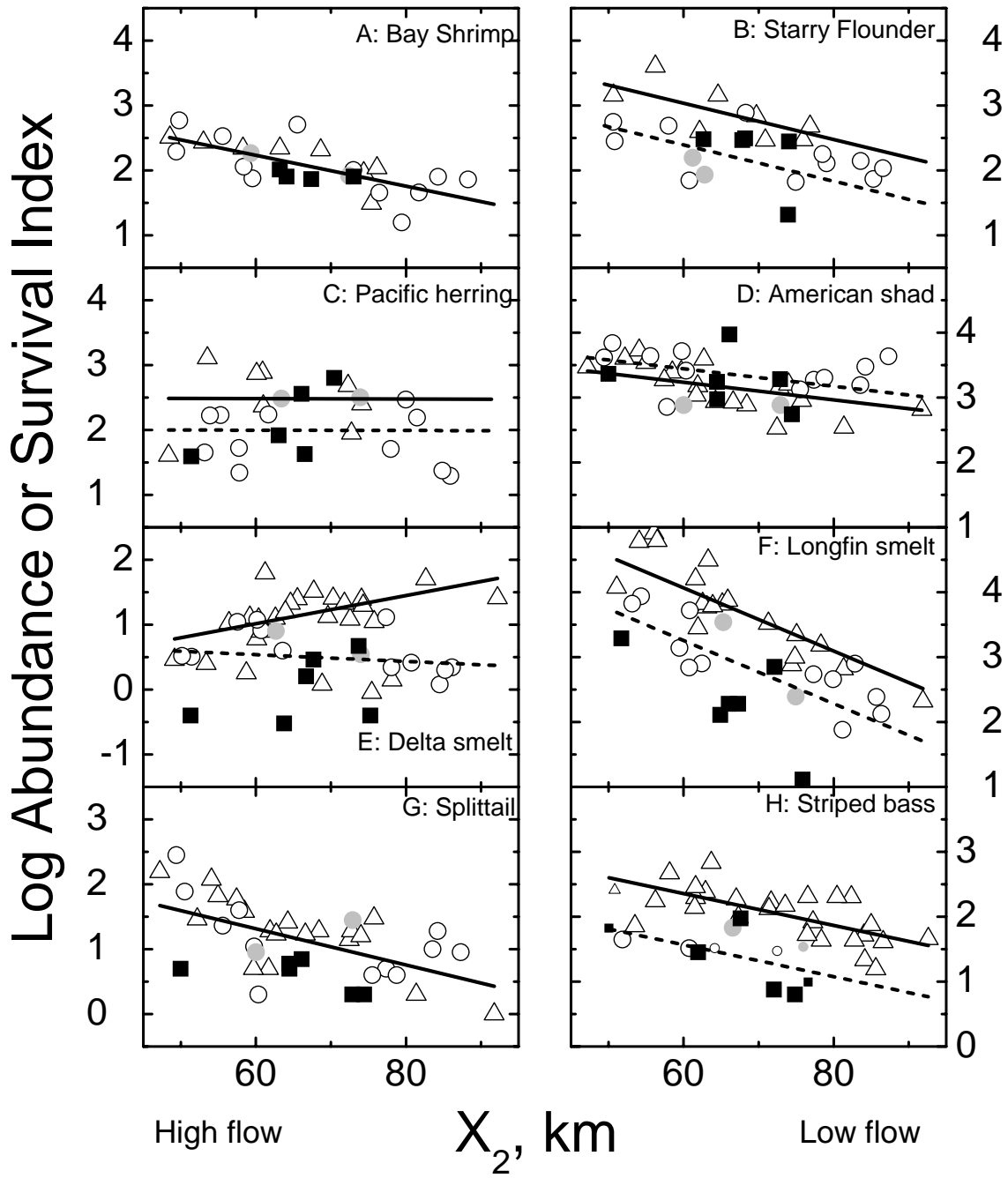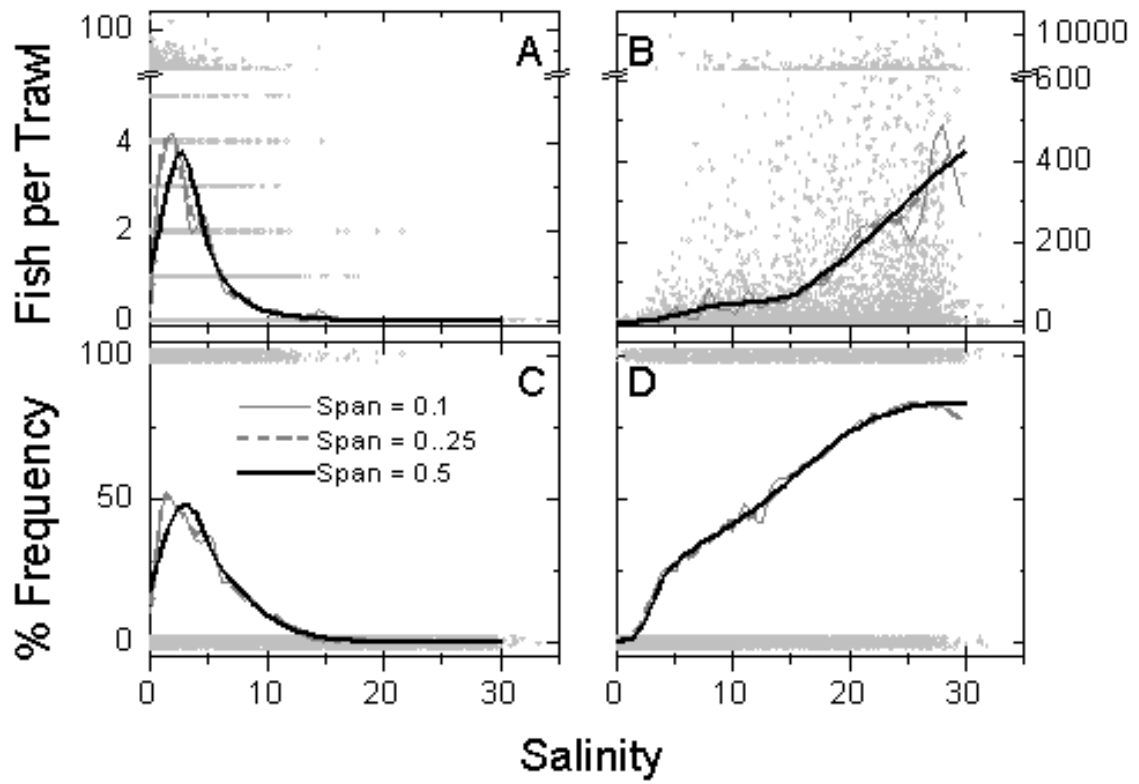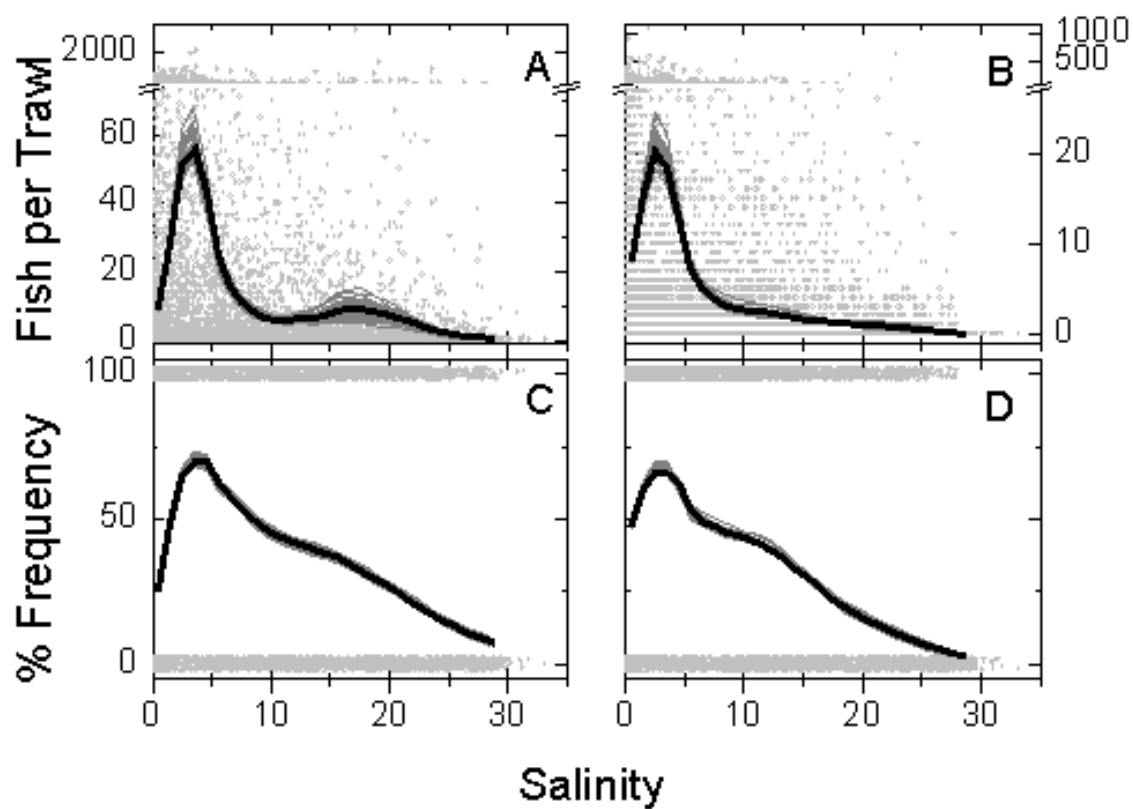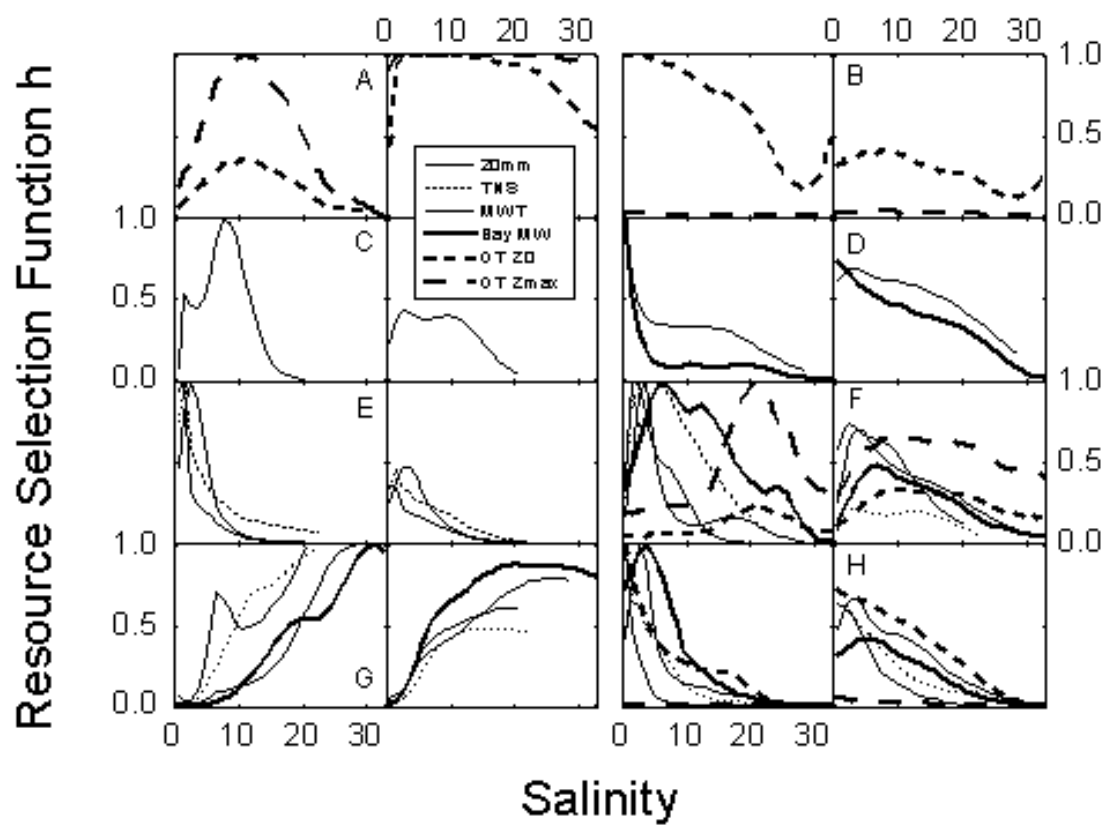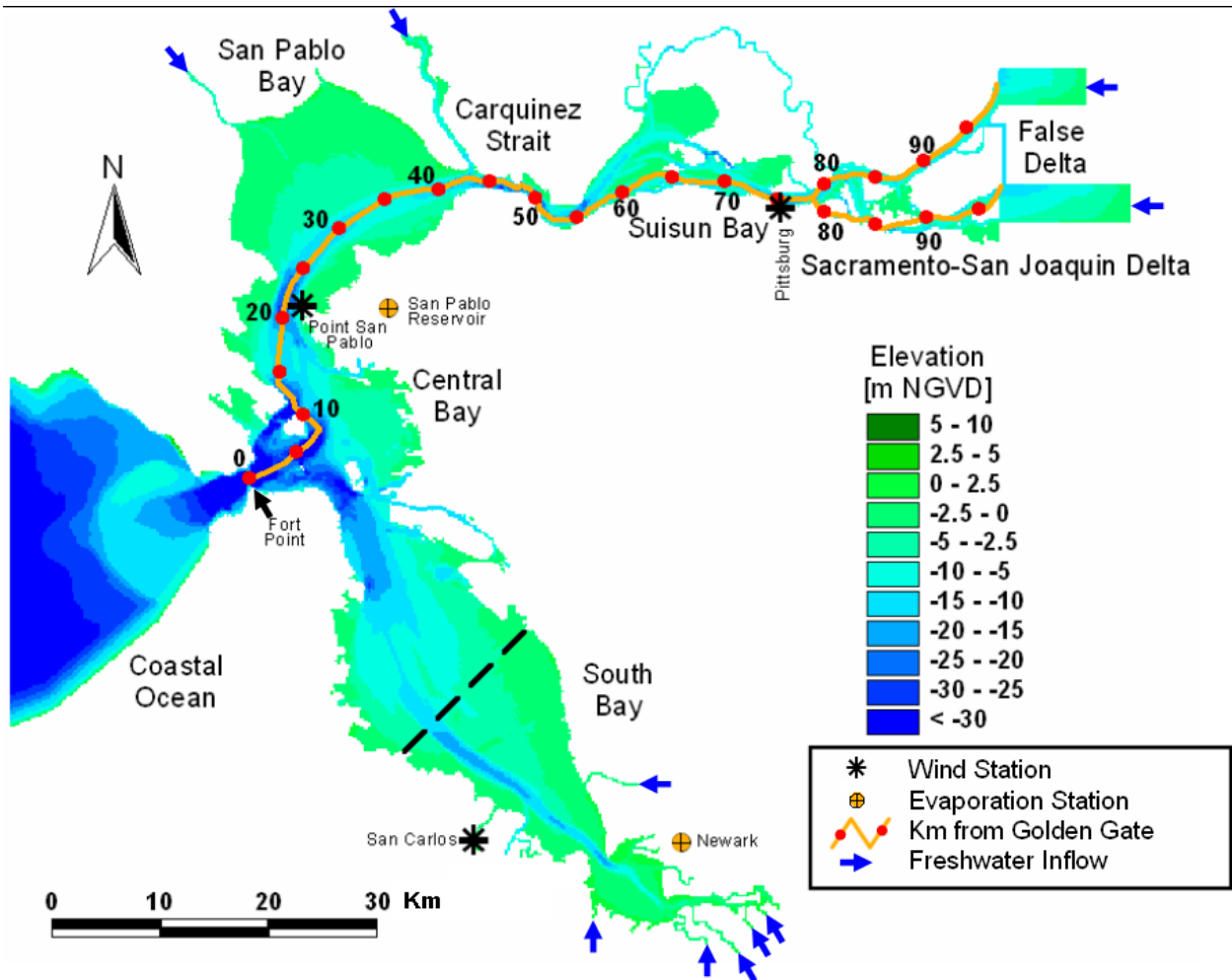
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9