

August 30, 2013



via email: interagencyecologicalprogram@gmail.com

Interagency Ecological Program Directors
980 9th Street, 14th Floor
Sacramento, CA 95814

Re: SWC, 2013 MAST Report Review

Dear IEP Directors:

The State Water Contractors (“SWC”) appreciate this opportunity to comment on the Draft IEP Mast Report (herein “MAST Report” or “Report”). The SWC recognize the significant effort put forth by your staffs to assemble the information contained in the MAST Report and understand the difficulty of such a significant undertaking. Acknowledging the importance of the MAST Report, the SWC have thoroughly reviewed the Report and have provided detailed and specific comments in an effort to describe where and how the Report could be strengthened. In order to thoroughly explain our comments, we have attached exhibits to this letter that include supporting graphs and citations. Since the Report is over 100 pages plus exhibits, we would request some flexibility regarding page limits, as without some flexibility the opportunity for a meaningful dialog is unnecessarily foreclosed.

While there is a lot of good information in the MAST Report, we have identified several areas where the report should be augmented, as follows.

- Several of the conclusions and recommendations are inadequately supported by the evidence presented.
- There are alternative hypotheses and conceptual models that should be included.
- The report should more explicitly acknowledge the uncertainties and limitations in the evidence presented.
- While the three stated objectives on page 20 are interesting questions, the use of data from only two dry-wet year combinations undermines the technical rigor of the analysis and evaluation of the conceptual model hypotheses.

DIRECTORS

David Okita
President

Solano County Water Agency

Dan Flory
Vice President

Antelope Valley-East Kern
Water Agency

Ray Stokes
Secretary-Treasurer

Central Coast Water Authority

Stephen Arakawa
Metropolitan Water District
of Southern California

Curtis Creel
Kern County Water Agency

Mark Gilkey
Tulare Lake Basin Water
Storage District

Douglas Headrick
San Bernardino Valley MWD

Joan Maher
Santa Clara Valley Water
District

Dan Masnada
Castaic Lake Water Agency

General Manager
Terry Erlewine

Addressing these shortcomings will greatly improve the MAST Report, making it a more objective and impartial description of our evolving understanding of delta smelt.

The SWC have organized their comments according to the six questions posed to reviewers.

MAST Report Questions 1 and 4: Are the objectives and/or questions the report seeks to address clearly described in the report? Are they fully addressed? Do the authors go beyond the objectives/questions? Is the report's organization effective? Is the title appropriate?

The stated goal of the MAST Report is to update previously developed conceptual models for delta smelt to organize our current understanding of the factors affecting delta smelt abundance and of delta smelt responses to these factors and then to use the updated conceptual model as a framework to a) organize and synthesize existing knowledge and b) formulate and evaluate hypotheses. (MAST Report, pp.20 and 27.) However, the MAST Report's narrow focus on four recent years artificially limits the strength of its analyses and conclusions. The agencies have collected decades of data. Looking at a very small subset of years reduces the chances that the causes of the apparent declines in abundance can be parsed out, and the result is an increased chance of spurious findings. At a minimum, the MAST Report could have examined why abundance in 2011 was apparently higher than the entire set of POD years from 2002-2010, as well as the years leading up to the POD.

Further information supporting these responses to questions 1 and 4 is provided in Appendix 1, attached.

Questions 2 and 5: Is the report objective? Is the tone impartial? Are uncertainties, alternative hypotheses and conceptual models, or incompleteness in the evidence explicitly recognized?

There are alternative hypotheses and observations that should be acknowledged. The following are specific examples of where the Report could be strengthened.

The conceptual model described in Glibert (2010) and Glibert *et al.* (2011) was not described in the MAST Report, even though it is particularly relevant to the development of the MAST conceptual model because food, predation, contaminants, and harmful algal blooms are listed as stressors for multiple delta smelt life stages. The findings in Glibert (2010) and Glibert *et al.* (2011) are also relevant to the discussion of regime shift, as they specifically discuss break points in the historic data where changes in nutrient ratios and changes in phytoplankton speciation occur. Finally, Glibert (2010) and Glibert *et al.* (2011) do not suggest that the POD decline was caused by a single variable (MAST Report at p. 18) rather their model links changes in nutrient ratios to multiple changes in the physical environment, many of which are likely effecting delta smelt and other POD species. Glibert *et al.*'s work could be viewed as an alternative to the hypothesis that changes in flow have been the primary driver of the multiple changes in the environment.

The MAST Report also does not adequately acknowledge that delta smelt are distributed across a range that is broader than just the LSZ. (MAST Report, p. 16.) The Dege and Brown 2004 paper is discussed but other literature suggesting the species distribution is quite broad is not discussed. (MAST Report, p. 16.) For example Sommer 2013 explains,

...the overall distribution of delta smelt habitat is much broader. The surveys do not necessarily capture the extremes of distribution and habitat shifts among years. Our analysis showed that delta smelt habitat is often located well downstream of the Delta, commonly Suisun Bay....”

Similarly, the MAST Report states that delta smelt use the upper estuary for spawning and rearing, but it does not acknowledge that spawning distribution varies and is not necessarily limited to the upper estuary. (MAST Report, p. 16.) The MAST Report should also acknowledge Bennett 2005 which states, “In years of high freshwater discharge spawning distribution is broader encompassing most of the Delta, Suisun Marsh channels, and the Napa River....”

Further information supporting these comments, as well as other examples of where alternative hypotheses and observations should be acknowledged, is provided in Appendix 2, attached.

Questions 2 and 3: Are the data and analyses handled competently and applied appropriately? Are conclusions and recommendations adequately supported by evidence and analysis? If the report's content is based on unpublished results, are findings and conclusions properly attributed to an individual or a specific program or project.

There are a number of improvements in the statistical analyses that we would recommend. For example:

- Figures 41 and 42: A larger data set should have been used, representing a greater number of years. The problem with using fewer years is not just ignoring decades of data, but it is also that catch numbers in recent years have been so small that the index ratios are increasingly uncertain. A change in catch of just a few fish can cause significant changes in the index ratios, making interpretation of the ratios too uncertain to be meaningful.

The use of the 20mm survey is a further complicating factor. The 20mm survey is only able to sample larger larvae, which were necessarily spawned early in the season. Therefore, if most delta smelt are spawned either at the beginning or at the end of the season, half of the ratios in Figures 41 and 42 will be impacted.

- Figure 43: The Sacramento River plus San Joaquin River index on the x-axis represents the entire water year, and this occurs well before and well after the two surveys used in each abundance ratio on the y-axis. This is an inappropriate comparison.

The other major concern with Figure 43 is that it only uses data from 2002-2011, which means that 2012 and all of the data from the preceding decades are missing. The use of such a small subset of years greatly magnifies the chances of incorrect inferences. In Appendix 2 to these comments we attempt to recreate Figure 43 using a larger number of years; the result is an increasingly weaker statistical relationship as more years are added.

- Figure 44: The linear correlation between the SKT index and the previous FMWT index is problematic. The analysis should look at log SKT versus log FMWT so that large values do not dominate the results and so that we can see whether SKT is directly proportional to FMWT or not.

We performed this analysis and found that the SKT varies with the FMWT as $FMWT^{0.62}$ or fairly close to its square root. (See Appendix 3, attached.) This suggests that the FMWT varies much more than the SKT and is likely biased downward, particularly at low index values.

- Table 4: The MAST Report largely deferred to FLaSH on the topic of fall X2. However the Report does contain a calculated area of habitat based on McWilliams (not Feyrer 2010) to represent simple open water acres within certain salinity ranges for 2005, 2006, 2010 and 2011. The use of so few years of data is a violation of generally accepted statistical principles. We recreated the analysis considering an increasing number of years. The more years that are considered, the weaker the statistical relationship. (See Appendix 3, Attached.) As a result, the conclusion in the MAST Report that data generally support the fall X2 conceptual model is unsupported.

Further information supporting these comments, as well as other examples of where the analysis could be improved, is provided in Appendix 3, attached.

Question 6: What other significant improvements, if any, might be made in the report?

There is recent evidence that the existing surveys may not be representative of delta smelt abundance and distribution due to several factors including sampling time of day, vertical and lateral position of gear, turbidity, and tidal stage at time of sampling (Feyrer et al 2013; Bennett and Bureau 2011; Fullerton unpublished data). The MAST Report should acknowledge the limitations of existing surveys and incorporate into the conceptual model the potential role of survey bias or inefficiencies on abundance indices. The MAST Report should also identify an investigation of survey efficiencies and biases as a critical next step. Identifying and trying to quantify survey bias is a critical precursor to determining likely factors affecting species abundance.

Specific evidence of survey bias in the existing surveys is described in detail in Appendix 4.

Interagency Ecological Program Directors

August 30, 2013

Page 5

The SWC look forward to discussing the MAST Report with the authors, and would like to be involved in the development or future refinement of the MAST conceptual model. If the MAST Report authors have questions about the SWC comments, please feel free to contact our primary reviewers, as follows:

David Fullerton. Email: dfullerton@mwdh2o.com

Dr. Paul Hutton. Email: phutton@mwdh2o.com

Frances Brewster. Email: fbrewster@valleywater.org.

Sincerely,

A handwritten signature in black ink, appearing to read "T. Erlewine". The signature is fluid and cursive, with a large initial "T" and a long horizontal stroke.

Terry Erlewine
General Manager

Appendix 1

Questions 1 and 4: Are the objectives and/or questions the report seeks to address clearly described in the report? Are they fully addressed? Do the authors go beyond the objectives/questions? Is the report's organization effective? Is the title appropriate?

The stated goal of the MAST Report is to update previously developed conceptual models for delta smelt to include our current understanding of the factors affecting delta smelt abundance and of delta smelt responses to these factors and then to use the updated conceptual model as a framework to a) organize and synthesize existing knowledge and b) formulate and evaluate hypotheses. (MAST Report, p.20 and 27.) The updates to the conceptual models are an improvement over prior versions as we support the use of the Miller hierarchy approach as an organizing principle. However, we prefer Miller's original format since the MAST Report's version of the effects hierarchy obscures primary and secondary effects and omits several factors.

The report does use the updated conceptual models to organize existing knowledge in that the discussion is organized by environmental driver, habitat attribute and life stage, although the report deviates sharply from the conceptual models in its use of hydrology as the organizing principle for the analysis of new data by focusing only on two dry-wet year combinations. Why the two wet years of 2006 and 2011 were selected as being particularly informative for determining what is driving species abundance is unclear. While it is certainly appropriate to discuss flows as they relate to each life stage, it is inappropriate to highlight them over all other environmental drivers.

The MAST Report's narrow focus on four recent years also artificially limits the strength of its analyses and conclusions. As a result, the MAST Report results were largely inconclusive as to which factors are likely affecting delta smelt abundance. The agencies have collected decades of data. Looking at a very small subset of years reduces the chances that causes of the apparent declines in abundance can be parsed out, and the result is an increased chance of spurious findings. At a minimum, the MAST Report could have examined why abundance in 2011 was apparently higher than the entire set of POD years from 2002-2010, and in the years leading up to the POD. Assuming that the authors choose to retain the use of flows as the organizing principle, an examination of the historical water year types indicates that 1975-1976, 1981-1982, 1985-1986, and 1994-1995 were all wet years preceded by drier years (based on the Sacramento Valley Index). These years span both the pre- and post-*Potamocorbula* period. While still not constituting a strong statistical data set, addition of these years of data would strengthen the understanding of delta smelt population dynamics under this combination of flow conditions.

While the conceptual models contained in the MAST Report is an improvement over previous models, they are still too poorly defined to use as the basis for developing testable hypotheses. The models need to be more explicit about how and which driver and habitat attribute affects each process (e.g. survival, maturation, growth, fecundity). It would also be helpful to indicate our current understanding of the relative importance of each factor and the interactions between variables as well as the certainty of our knowledge and the potential magnitude of effects. MAST Report, p. 32, lines 711-712, states that “we consider all habitat attributes discussed here as equally important...” While this may be true, not all habitat attributes are equally limiting. The report should include some indication of which attributes may be limiting survival, growth, and reproduction.

There remain many foundational questions that should be captured in the conceptual models and translated into testable hypotheses. We cannot list all of the foundational questions in this comment letter, but would be pleased to discuss the types of questions that need to be addressed in a follow up conversation.

Finally, the MAST Report should also acknowledge the potential for survey bias as well as the existence of random error- particularly in years with low catch. The MAST Report appears to assume that adult and larval survey data can be used without any consideration of survey bias or uncertainty. As there is evidence of bias and random error in the survey data, see Appendix 4, the MAST conclusions based on consideration of index ratios is problematic.

The following are specific recommendations for further improving the conceptual model diagrams:

Comments on MAST Report Figures 8-11

- The variable “food availability/visibility” is appropriate, but visibility should be directly, not indirectly, linked to turbidity.
- The MAST Report’s “food production/retention” variable is directly linked to turbidity and hydrology, but it should also be indirectly linked to ammonium levels and/or N:P ratios.
- There should also be a variable that includes food quality, rather than just quantity. Food quality could be heavily influenced by N and P, as well as past clam invasions. Proximity to wetlands may also affect food quality and quantity (Murphy *et al.*, in press).
- Predation risk is properly linked to predator abundance and turbidity, but it may also be indirectly linked to N:P ratios (Glibert *et al.* 2011). To the extent predator populations could be impacted by stoichiometric shifts, more predators means more risk.
- The migration variable for adults assumes that delta smelt migrate. This assumption may not be valid given the finding that a sometimes significant portion of the population are year-round residents in the Cache Slough/Sacramento Deep Water Ship Channel region

(Jim Hobbs presentation at EET 8/22/2013). A more appropriate habitat attribute might be spawning cue which should also include a temperature factor.

- Entrainment risk at the adult life stage is not just related to hydrology and exports, but also turbidity.
- Turbidity is not just a function of hydrology, but also of past suspended sediment loading patterns and wind speed. Suspended sediment loading is in turn partially determined by the weather, but also by historical land use patterns (*e.g.*, gold rush sediment, changes in upstream vegetation).
- Model should include considerations of geography or physical habitat or bathymetry of spawning substrates. The current model assumes that geography is fixed; but it's not fixed and the BDCP envisions making major changes to physical habitat. Based on Murphy et al. (in press), physical habitat variables should include "availability of tidal wetlands" and "availability of high quality spawning substrates" and perhaps availability of "bathymetric up-wellings."
- The temperature variable should explicitly recognize that favorable temperatures may allow for additional clutches of eggs.

Appendix 2

Questions 2 and 5: Is the report objective? Is the tone impartial? Are uncertainties, alternative hypotheses and conceptual models, or incompleteness in the evidence explicitly recognized?

The report makes a good effort at summarizing the information and conceptual models objectively and impartially; however, there are several places where the impartiality could be improved, for example:

- At its foundation, the basic structure and the objectives of the report place undue importance on hydrology as the key driver of delta smelt abundance. The fact that the report focused specifically on the comparison between the wet years of 2006 and 2011 implies that the authors assume wet hydrology is a key driver of abundance. In fact, the second report objective on page 20 asks, “why did delta smelt fail to respond to wet conditions in 2006?” This question pre-determines that wet conditions should increase delta smelt abundance.
- Several statements do not objectively describe the influence of CVP/SWP operations compared to other anthropogenic influences on the estuary. For example:
 1. Statement in MAST: “These alterations include diking and draining of the historical wetlands, large scale water diversions from the southwestern Delta into the California State Water Project (SWP) and the Federal Central Valley Project (CVP), inputs of contaminants, and species introductions.” (MAST Report at p. 15, lines 337-339.)

This list is incomplete and inappropriately focused on the SWP/CVP diversions when up-stream and in-Delta diversions have also greatly altered the estuary. Besides the changes identified above, the list should include: deepening and straightening of channels including the Sacramento River, and the Sacramento and San Joaquin Deep Water Ship Channels, significant increases in agricultural development (and associated water use) throughout the Sacramento Valley and in the Delta, and the construction of the extensive network of rip-rapped levees throughout the Delta. While many species are introduced; only the ones that are able to proliferate have altered the estuary.

2. Statement in MAST: “Moyle and Bennett (2008) and Baxter et al. (2010) suggest that the SFE, particularly the Sacramento-San Joaquin Delta has undergone an ecological regime shift. Specifically, the Delta has changed from a pelagic-based estuarine system with variable salinity on seasonal and annual scales to a system reminiscent of U.S. southeastern reservoirs. In the present system an invasive aquatic macrophyte (*Egeria densa*) dominates the littoral areas of many areas of the Delta and provides ideal habitat for many invasive fishes...invasive clams...and [a] current management of water for agricultural, industrial and urban purposes is focused on stabilizing flow and salinity regimes to optimize water exports by the federal Central Valley Project (CVP) and State Water Project (SWP).” (MAST Report at p. 18, lines 390-401.)

The MAST Report states that this theory of a system reminiscent of a southeastern reservoir was “suggested” by the cited references, however the document is written as though it is a scientific fact. It should be noted that the cited references did not establish that the flow regime had been stabilized by water project operations, nor do the references establish that changes in water project operations resulted in the laundry list of identified changes in the environment.

The SWC have completed an analysis of flow and salinity trends. The preliminary analysis was presented during the SWRCB Phase II workshops last fall. That analysis indicates that flows from the Sacramento River continue to exhibit significant variability. Comparatively speaking, the San Joaquin River exhibits significantly less variability, but that change in the San Joaquin River system cannot be solely attributed to the CVP-SWP, as upstream water use is a significant contributor.¹

In addition, optimizing exports by CVP/SWP is not the sole intent of water management actions. In-Delta water uses also dictate water management actions to maintain fresher water conditions.

3. The MAST Report describes flows from north Delta to OMR via the artificial delta cross-channel. (MAST Report, p. 48, lines 1060-1063.) Report should recognize that flows also pass through the natural Georgiana Slough.
4. The MAST Report needs to clarify that pumping by SWP and CVP are sufficient to cause the loss of ebb tide flows only in some areas and at some times. (MAST Report, p. 48, lines 1063-1066.)

There are several places where a more balanced presentation is needed, including:

- Statement in MAST: “The other native osmerid fishes commonly found in the upper SFE is longfin smelt (*Spirinchus thaleichthys*) which regularly spawns in the Delta.” (MAST Report at p. 16, lines 348-349, see also, p. 17, lines 383-385.)

First, the relevance of the reference to longfin smelt in a paper about delta smelt is unclear. Longfin smelt have very different biology than delta smelt, primarily being a marine species. Second, it is true to say that some longfin smelt spawn in the Delta, but it isn't accurate to imply that all, or even most, longfin smelt spawn in the Delta. There is evidence that many longfin smelt spawn in the Napa River and farther downstream. (See *e.g.*, COE trawling program data for Napa River in 2001 and 2003.)

- Statement in MAST: “Most delta smelt complete the majority of their life cycle in the low salinity zone (LSZ) of the upper estuary and use the freshwater portions of the

¹ The SWP has no facilities on the San Joaquin River system.

upper estuary primarily for spawning and rearing of larval and early post-larval fish.” (MAST Report at p. 16, lines 356-359.)

The statement that delta smelt complete the majority of their life cycle in the LSZ should be further qualified. Dege and Brown 2004 describe the “centroid” of the delta smelt population as occurring in the LSZ. However, as Sommer 2013 explains:

“...the overall distribution of delta smelt habitat is much broader. The surveys do not necessarily capture the extremes of distribution and habitat shifts among years. Our analysis showed that delta smelt habitat is often located well downstream of the Delta, commonly Suisun Bay...one of the most surprising discoveries was their presence in the Napa River...Hobbs et al. (2007) found that use of habitat in this region results in a unique chemical signature in the otoliths of delta smelt and revealed that the portion of fish that use the Napa River can be substantial (e.g., 16% to 18% of the population in 1999).

There is also some question regarding the extent that delta smelt spawning and rearing is limited to the freshwater portions of the upper estuary. Even Bennett (2005)² indicated that spawning distribution changed from year to year, stating, “In years of high freshwater discharge spawning distribution is broader encompassing most of the Delta, Suisun Marsh channels, and the Napa River [cite omit].” Bennett’s description is consistent with that articulated by Moyle 2002³ and 1992⁴, reflecting previous observations reported by Radtke (1996), Wang (1986, 1991) and Wang and Brown (1993).

This migration hypothesis is further questioned by Murphy and Hamilton (in press),⁵ where the authors suggest that the delta smelt population expands in all directions seeking fresher water for spawning and rearing rather than limiting their search for fresher water only to upstream locations.

- Statement in the MAST: “...leading to concerns that the population might now be subject to “Allee” effects (Baxter et al. 2010) and have lost its resilience, meaning its ability to recover to higher population abundances when conditions are suitable...Unfortunately, the increase in delta smelt abundance was short-lived and did not carry over into the following year-class in 2012, a drier year.” (MAST at 19, lines 410-412.)

The MAST report needs to provide a more balanced presentation of this issue. Baxter *et al.* 2010 presented the potential Allee effect as an untested hypothesis so the Mast

² Bennett WA. 2005. Critical assessment of the delta smelt population in the San Francisco estuary, California. San Francisco Estuary and Watershed Science 3(2).

³ Moyle PB. 2002. Inland fishes of California. University of California Press. Berkeley, CA.

⁴ Moyle, P.B, Herbold B, Stevens D.E, Miller, L.W. 1992. Life history of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.

⁵ The paper is titled, “Eastward migration or marsh-ward dispersal: understanding seasonal movements by delta smelt.”

report needs to be cautious about presenting this concept without appropriate qualifying statements. We are unaware of any published analysis that tests the Allee hypothesis so significantly more work would need to be done before it could be put forth as a potential concern. The MAST Report does properly point out that the increase in abundance in 2011 does not support the Allee hypothesis.

The MAST Report also seems to assume that since 2012 was drier than 2011, the comparative dryness of 2012 is the reason the apparent abundance increase in 2011 did not carry over to 2012. However, there is no evidentiary support provided for the expectation that the apparent 2011 abundance increase should have carried over to 2012. Conversely, if the MAST expectation regarding 2012 abundance is based on Feyrer *et al.* 2007, and an increase in abundance was expected in the Summer Townet Survey, based on high fall 2011 outflows, that should have been explicitly stated. If that is the case, then the Feyrer *et al.* 2007 analysis should have been discussed, along with its limitations.

There are several places where uncertainties and the incompleteness of the evidence should be explicitly recognized. For example:

- Statement in the MAST: “Longfin smelt, age-0 striped bass (*Monrone saxatilis*), and threadfin shad (*Dorosoma petenense*) decline simultaneously with delta smelt...” (MAST Report at p. 17, lines 383-385.)

The MAST Report should acknowledge that the various surveys, or population indices, suggest different abundance trends. For example, the Otter Trawl data suggests that longfin smelt abundance has not declined since the 1980s, while the FMWT data suggests a significant decline in longfin smelt abundance during the same time period. The fact that different surveys suggest different abundance trends indicates that some surveys are be more effective at sampling longfin smelt than others, which is something that needs to be investigated before one survey can be relied on more heavily than another. It is also an uncertainty that needs to be acknowledged in the MAST Report.

One possible explanation for differences in the surveys is a change in species distribution, either within the water column or between areas that are sampled and those not sampled. The surveys are limited in their ability to identify changes in species distribution because the surveys monitor the same locations each year. There are examples of where this has occurred. For example, striped bass age-0 fish have likely changed their distribution away from areas sampled by the FMWT, moving from channels to shoal areas (Sommer *et al.* 2011)⁶. This observation is further substantiated by the survey data for age-1 fish, which did not show the same decline (Sommer *et al.* 2011). This change in age-0 striped bass distribution should be discussed in the MAST Report as an uncertainty about the extent to which the age-0 striped bass have declined.

⁶ Sommer, T., Mejia, F., Hieb, K., Baxter, R., Loboschfsky, E., Loge, E. 2011. Long-term shifts in the lateral distribution of age-0 striped bass in the San Francisco Estuary. Transactions of the American Fisheries Society, v. 140, pp. 1451-1459.

The MAST Report should acknowledge the limitations of the surveys and indicate that part of the testing of the MAST Report’s conceptual model should include evaluating the surveys (*i.e.*, testing efficiencies, changes in species distribution, etc.)

- Statement in the MAST: “Since the beginning of the POD in 2002, the delta smelt population indices have often been at record lows....” (MAST Report at p. 19, lines 409-410.)

The MAST Report should acknowledge the limitations of the surveys and the evidence of survey inefficiencies. For example, Jon Burau and Bill Bennett have observed that delta smelt move to the sides of the channel during the ebb tide and to the middle of the channel during the flood tide. Feyrer *et al.* 2013⁷ confirmed this behavior. What this suggests is that surveys on the flood tide are going to catch significantly more fish where delta smelt are present, and that surveys on the ebb tide are going to fail to successfully sample delta smelt even when they are present.

There is evidence of other survey errors and inefficiencies that may have been particularly acute during the POD years. Please see Appendices 3 and 4.

Alternative conceptual models are not accurately described or appropriately recognized.

- Statement in MAST: “...although some researchers have suggested that single variables may have particular or even primary importance (*e.g.*, Glibert *et al.* 2011).” (MAST at p. 18, lines 389-390.)

Glibert *et al.* 2011⁸ described a regime change in nutrient ratios and explained how that change could cause a wide range of biological changes in the Bay-Delta, like those already being observed (*e.g.*, changes in dominant species of zooplankton and fishes (rise in centrarchids), increased blue-green algae and SAV, and increases in clam abundance). Glibert *et al.* did not suggest that the observed declines in delta smelt abundance indices were caused by a single factor rather Glibert *et al.* described a model of how changes in nutrient ratios could have led to multiple changes in the environment.

The model described in Glibert *et al.* is actually an alternative model to the single-variable model described by Moyle and Bennett (2008) and the POD Synthesis Report, referenced immediately below, which suggests that all of the aforementioned changes were caused by a change in salinity and flow patterns rather than changes in nutrient ratios.

⁷ Feyrer, F., Portz, D., Newman, K.B., Sommer, T., Contreras, D., Baxter, R., Slater, S.B., Sereno, D., Van Nieuwenhuyse. 2013. SmeltCam: Underwater Video Codend for Trawled Nets with an Application to the Distribution of the Imperiled Delta Smelt. PLoS ONE 8(7):e67829. Doi:10.1371/journal.pone.0067829.

⁸ Glibert, P.M., Fullerton, D., Burkholder, J.M. Cornwell, J.C., Kana, T.M. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco Estuary and Comparative Systems. Reviews in Fisheries Science, 19(4): 1-60.

The entire nutrient topic should be further developed in the report and we are happy to provide assistance in this area. There is a tremendous amount of published research and available data in SFE as well as elsewhere in the world that could be included and evaluated in this report.

- Statement in the MAST: “One hypothesis to explain these changes in fish population dynamics is that lower prey abundance reduced the system carrying capacity...” (MAST Report, p. 66, lines 1477-1479.)

This is only one hypothesis, and it has not been shown to be any more possible than any other hypothesis. Another hypothesis is that abundance of these species was never responding to outflow, but rather to a factor related to outflow such as ammonium concentration or the ratio of nitrogen to phosphorous (Glibert *et al.* 2011).

- Statement in the MAST: “...the decline in *P. forbesi* in the Suisun region may be related to increasing recruitment failure and mortality...in this region due to...entrainment of source population in the Delta...”

While this hypothesis has been frequently cited, we are unaware of any evidence that *P. forbesi* populations in the Delta would make it to the Suisun region, even if the CVP/SWP pumps were not operating.

- Statement in the MAST: “Currently, *E. affinis* abundance peaks in spring [cite omit] coincident with hatching delta smelt. *E. affinis* abundance has been negatively related to X2 since the clam invasion [cite omit]. When X2 is “high” outflow is low and *E. affinis* densities are low. These lines of evidence suggest that the first feeding conditions may improve in spring with higher outflow.”

The negative relationship between *E. affinis* and X2 is described, suggesting that higher outflow increases abundance of this prey item for delta smelt. However, *E. affinis* is also related to nutrient forms and ratios (Glibert *et al.* 2011).

Appendix 3

Questions 2 and 3: Are the data and analyses handled competently and applied appropriately? Are conclusions and recommendations adequately supported by evidence and analysis? If the report's content is based on unpublished results, are findings and conclusions properly attributed to an individual or a specific program or project?

While the report includes an impressive compilation of references to published literature, it still makes numerous statements that are unsupported, many of which could be supported. For example, page 35, lines 782-784; page 784, line 784; page 35, lines 787-790; page 35, line 790.

Specific comments regarding the use of data is provided, below:

- **Comments on MAST Report Figures 41 and 42**

There is inadequate scientific rationale for limiting the years in the analysis to the years since 2002. The MAST Report justified the use of the post 2002 years because that is when the SKT survey started. However, we have data from decades earlier; that data is relevant and should be utilized. The analysis could go back to 1995 and use the 20 mm survey. The analysis can go back to the 1960s and use the FMWT and STN. The problem with using fewer years is not just ignoring decades of data, it is also that catch numbers in recent years have been so small that the index ratios in the Figures 41 and 42 are increasingly uncertain. A change in catch of just a few fish can cause significant changes in the index ratios in Figures 41 and 42, which makes interpretation of the ratios too uncertain to be meaningful.

The way the 20mm survey (larval) is calculated is also a concern for purposes of this analysis because larvae are generally not detected in the survey until they are 20mm. Since the smaller larval delta smelt will not be detected,¹ the survey is only measuring the larger larvae, which were likely spawned earlier in the season.² Therefore, if delta smelt spawn earlier or later or if the spawning window is short or long in a particular year, the ratios in Figures 41 and 42 will be greatly impacted. This problem may well be distorting the data in Figures 41 and 42. It is worth noting that the height of the orange bar (larvae/previous adults) is inversely related to the height of the green bar

¹ The MAST Report observes that the 20mm survey begins before the delta smelt egg clutches have even hatched based on temperature. (MAST Report at 94, lines 2098.) The laying window based on temperature does not close until June or July. Given that eggs may not hatch for 35 more days and then are not large enough to be detected in the survey for weeks after that, the 20mm survey may not be an accurate measure of larval abundance? For example, the 2013 20mm survey index used only data from April and May. This would represent delta smelt that were laid as early as February through perhaps early April. But according to the MAST Report, the delta smelt spawning window in 2013 extended until June and these smelt would not have been detectable until July or August, a full two to three months beyond the coverage of the 20mm survey index.

² MAST Report, p. 81, line 1805, observes the delta smelt's ability to spawn twice. The practical effect is that the 20 mm survey is subject to enormous bias as with double spawning there will be many delta smelt too small to be captured in the 20mm survey. The MAST report should acknowledge this limitation and the uncertainty it creates in the use of the data.

(juveniles/larvae). This means that in Figures 41 and 42 when it appears the larvae phase has had terrible survival, the subsequent survival from the larval to juvenile phase is typically great. This could be density dependence, but another explanation is that the 20mm index is not representative of actual abundance,³ and giving inaccurate measurements. The STN may be more accurate (or at least flawed in different ways) so that errors in the 20mm survey are partially corrected by the time of the STN. However, that there is strong evidence of size selection bias in the STN Index caused by inconsistency in the start date of the STN each year. Figures A-B, below, illustrate this point.

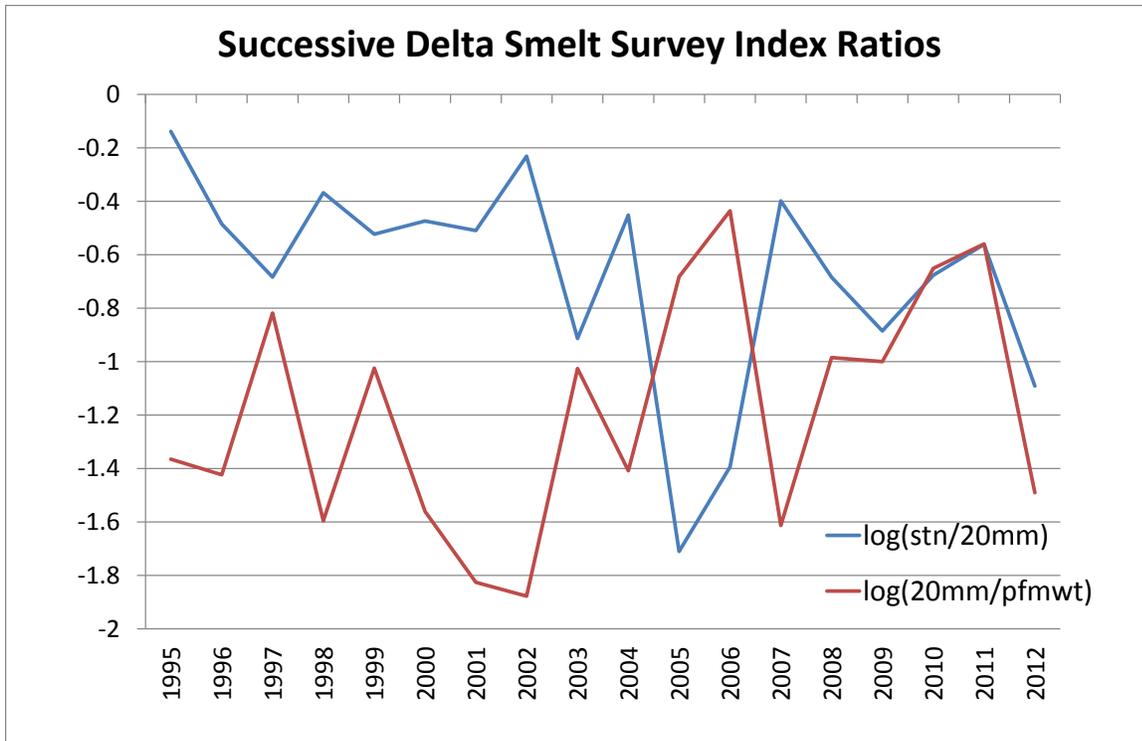


Figure A. Log STN/20mm survey compared to log 20mm/previous FMWT for years 1995 through 2012.

³ MAST Report at p. 92, lines 2044-2064, does not acknowledge that the 20mm survey may not be representative of larval abundance.

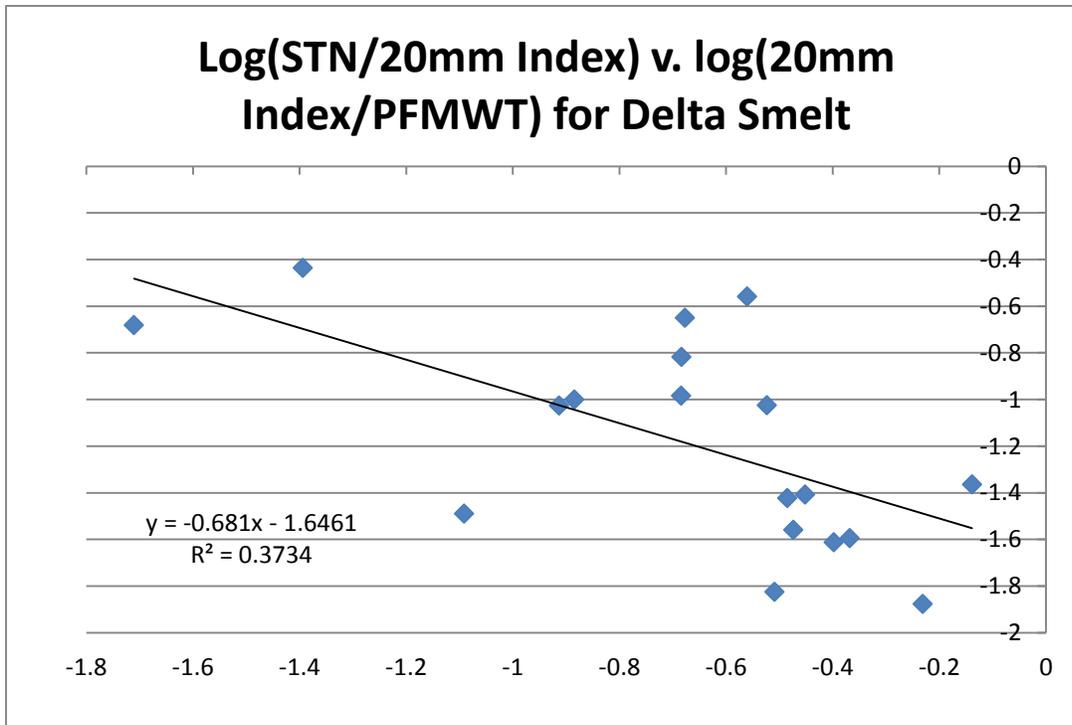


Figure B. Log (STN/20mm index) v. log (20mm index/previous MWT) for delta smelt.

Figure A shows successive index ratios for delta smelt in individual years. Figure B shows the same data plotted as a dot plot. The pattern is very clear. When survival from FMWT to 20mm is poor, survival from 20mm to STN is good and vice versa. This is either density dependence (and this is very unlikely at current abundance levels) or it is survey errors. If it is survey error, then the 20mm index may not be useful as an index of delta smelt larval abundance and should either be corrected or abandoned.

Again, the fact that we can use FMWT and STN to detect errors in the 20mm survey does not necessarily mean that FMWT and STN are without problems, but does suggest that the errors in these surveys are probably not fully correlated with the errors in the 20mm survey.

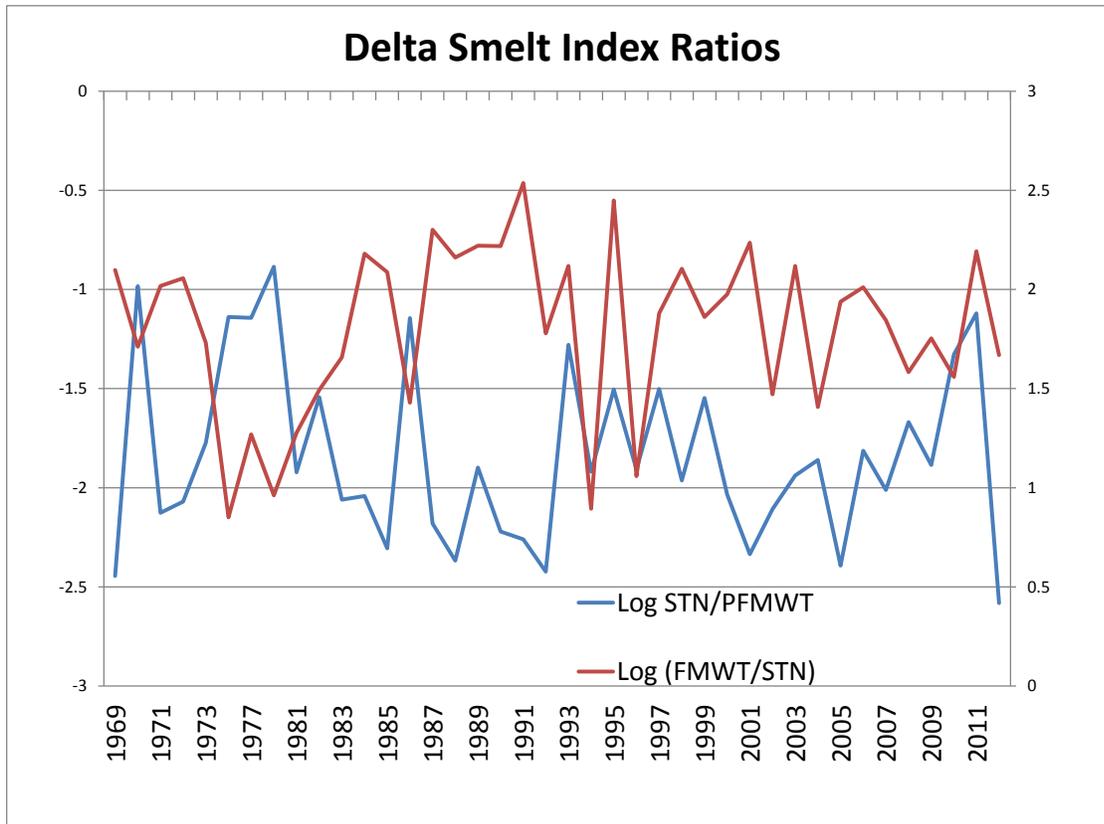


Figure C. Delta Smelt Index Ratios. Log STN/previous FMWT comparison to long (FMWT/STN).

By a similar process we can look for error in the STN survey. Figure C shows successive $\log(\text{STN}/\text{PFMWT})$ and $\log(\text{FMWT}/\text{STN})$ values since 1969. Clearly, the two ratios tend to move in opposite directions. Either this is some form of density dependence (though it is hard to see how density dependence could have applied during the low abundances of the 1980s) or it is an indication of a bias/error relationship. That is, bias or error in one survey (either FMWT or STN) tends to get corrected in the succeeding survey because the errors in the two surveys are not well correlated with each other.

In fact, the 20mm Index/PFMWT index provides fairly strong evidence that FMWT survey error jumped during the POD years, potentially exaggerating the estimated decline in delta smelt abundance. Figure F shows these ratios from 1995 – 2013. The ratios took a significant upward jump almost exactly when the POD occurred, with the 2004 FMWT and 2005 20mm survey. In other words, supposed survival from adults to larvae took a major leap upward during the POD years (years supposedly very bad for smelt) or the FMWT Index has been biased downward during the POD years or the 20 mm survey has been biased upward during the POD years. Given that the SKT also suggests that the FMWT Index has been biased downward during the POD years, FMWT bias may be the most likely explanation. In turn, if the FMWT index is suffering from significant bias or error, then unless that bias remains constant from year to year it will be difficult to parse out biological conclusions simply by looking at index ratios – the values are simply too uncertain.

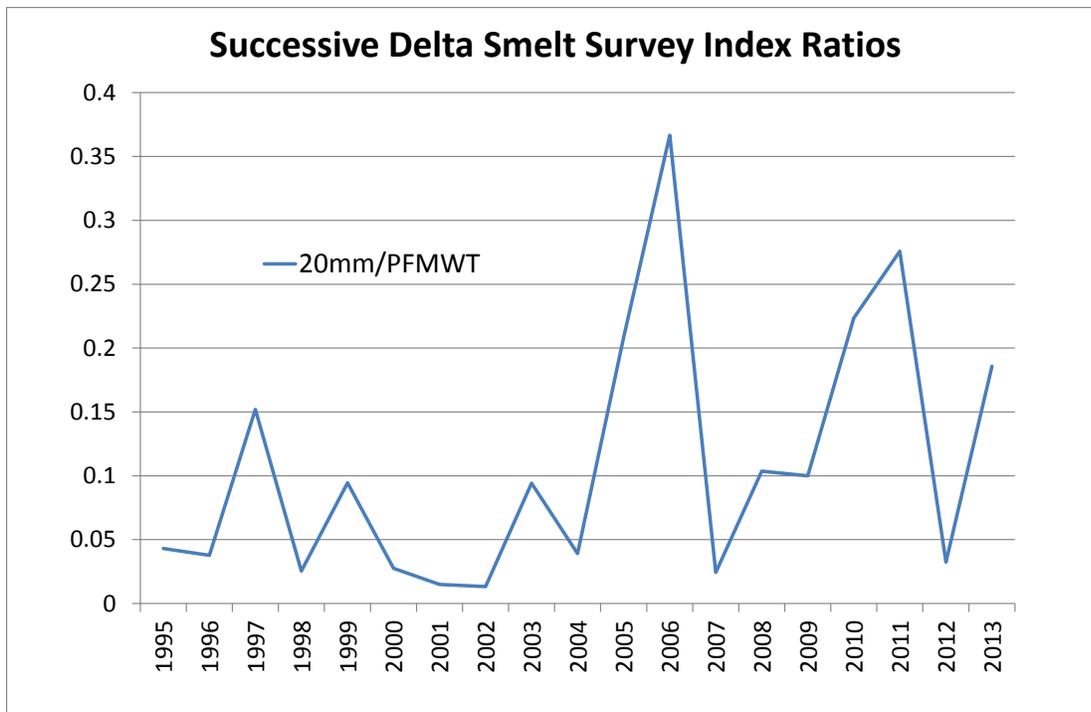


Figure F. Successive Delta Smelt Survey Index Ratios, 1995-2013.

The MAST Report’s search for biological meaning by looking at successive survey ratios is fraught with problems unless and until survey errors are examined and corrected in the data.

- **Comments on MAST Report Figure 43⁴**

There are multiple technical errors underlying Figure 43 that undermine the utility of the comparison. First, the Sacramento plus San Joaquin River index on the x-axis represents the entire water year, and much of this data occurs before or after the two surveys used in each abundance ratio on the y-axis. This is not an appropriate use of data in a statistical analysis.

Second, only data from the years 2002 – 2011 are used in the analysis, which of course means that data from the year 2012 is missing, as is all data from the preceding decades. The use of such a small subset of years greatly magnifies the chances of incorrect inferences. As an example, we have attempted (without complete success) to reproduce the larvae/prior adults data points shown in Figure 43 for the years 2002 – 2011. We used FMWT instead of SKT.⁵ We do not get the same fit using the relationship with the Sacramento + San Joaquin River flow index (Figure D) (although there still is a good relationship). However, once we add in additional years of data (1995 – 2001, 2012 – 2013), the relationship virtually disappears (Figure E). What appeared to be a strong

⁴ This MAST Report figure is unpublished and authorship is not attributed to any individual or entity.

⁵ We used the FMWT so we could recreate the analysis considering a greater number of years.

relationship now becomes (at best) a very weak relationship. This is a good example of how limiting the number of years can lead to incorrect inferences.

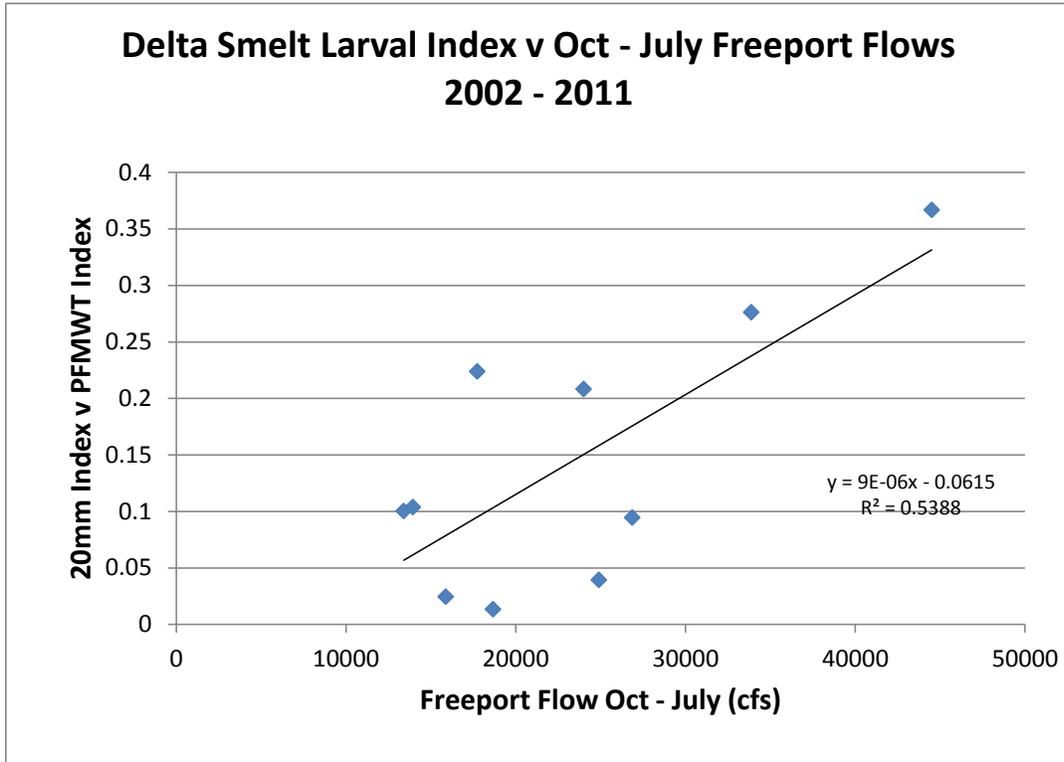


Figure D. Delta Smelt Larval Index (20 mm index v. previous FMWT index) v. October-July Freeport Flows (2002-2011).

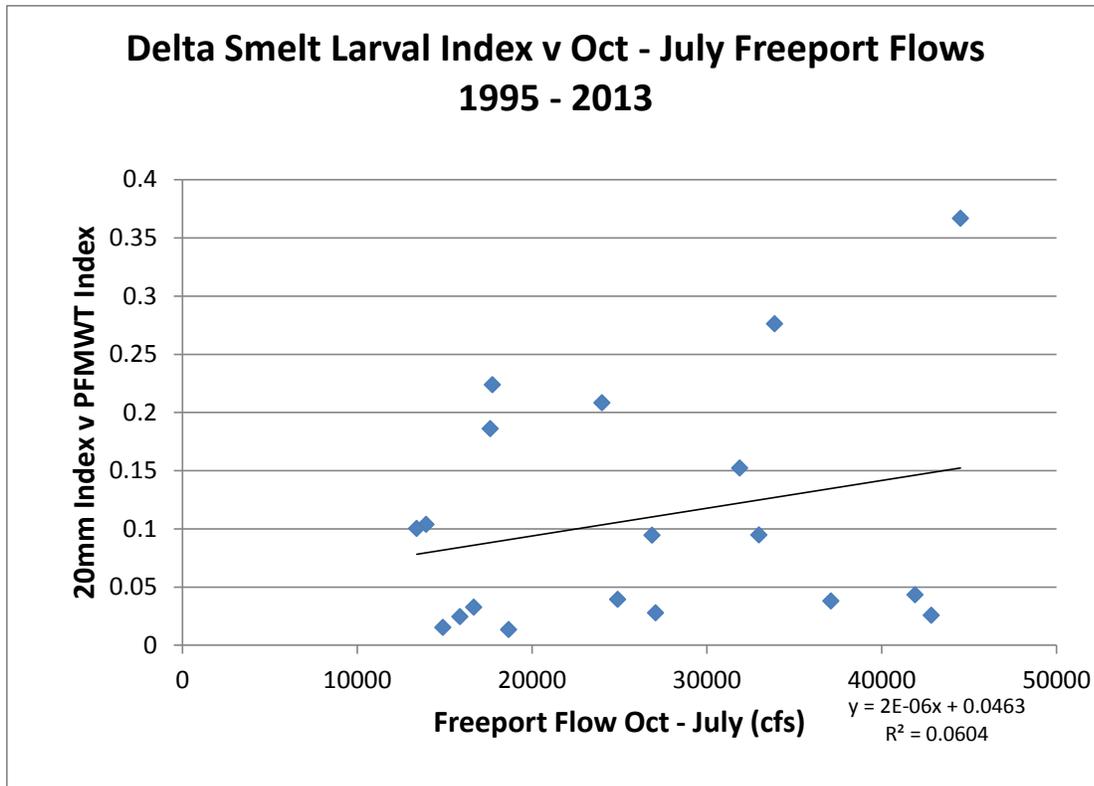


Figure E. Delta smelt larval index v. October-July Freeport flows, 1995-2013.

- **Comments on MAST Report p. 106, lines 2315-2335**

The analysis only considers temperature data in four specific years. As a result of using only a few years of temperature data, the MAST Report was unable to reach a conclusion. This illustrates the problem with ignoring decades of temperature data which could have been used to analyze the impact of temperature on survival.

- **Comments on MAST Report p. 107, lines 2340-2342**

It is unclear why striped bass are assumed to be a major predator. The more interesting analysis would be testing whether the centrarchids and/or inland silversides, which have increased significantly in abundance during the last decade, are causing changes in species abundance. The MAST Report just describes what happened in individual years but provides no insight into whether predation is or may be causing changes in abundance.

- **Comments on MAST Report p.77, lines 1725-1727 (see also, p. 69, lines 1539-1540)**

Sweetnam (1999) is outdated and not relevant to a discussion of delta smelt length during the POD years. FMWT delta smelt lengths have nearly returned to levels that existed prior to the drop in lengths recorded around 1992. See Figure H. It should also be acknowledged that prior to about 1992, not all delta smelt were routinely measured for

length. As there were no standard procedures for measuring delta smelt, there is the possibility of selection bias (*e.g.*, the personnel measuring the fish might have tended to grab larger than average fish). The Summer Townet dataset also has length data. The STN length data from July does not support the pattern identified in the MAST (a collapse in smelt length after the early 1990s). Average STN length is shown in Figure I. Figure I suggests that lengths may have been slightly enhanced during the 1980s, but that lengths from the 1990s to the present are similar to lengths seen during the 1970s. Therefore, there is no evidence of a collapse in length and the so-called Big Mama hypothesis first proposed by Bennett should be rejected.

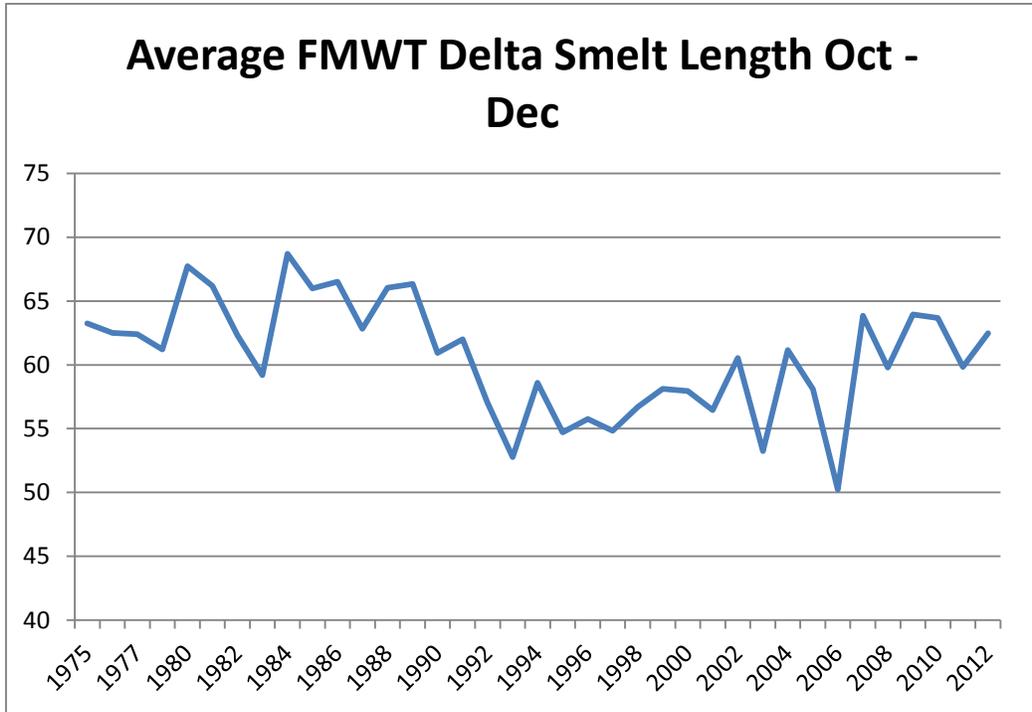


Figure H. Average FMWT delta smelt length, October- December for the years 1975-2012.

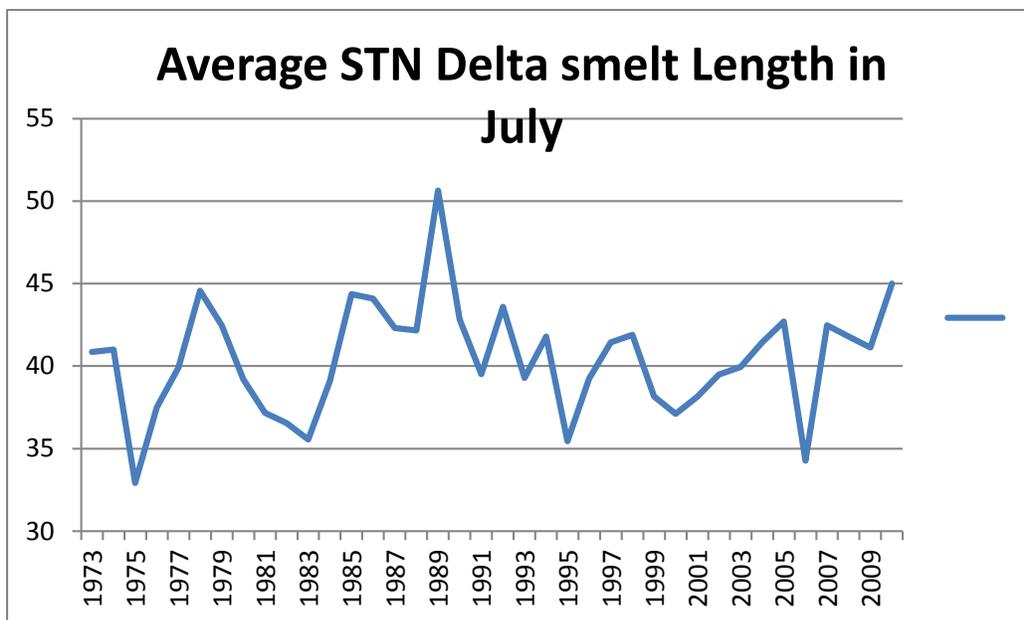


Figure I. Average STN delta smelt length in July, 1973-2009.

- **Comments on Mast Report Figure 24, p. 101, lines 2244-2254**

We are unable to find Figure 24. However we are concerned about the conclusions contained in the MAST Report that appears to be based on a correlation with four data points. A correlation using four data points is meaningless, suggesting a misapplication of standard statistical practices. In addition, many things are correlated with OMR flows; so even if the correlation described here existed, it would not be particularly informative and interpreting the results would be difficult.

The referenced discussion again refers to Figure 43, which was discussed above.

In light of the misapplication of standard statistical principles, the strong conclusions at lines 2250-2254 are **not supported by the analysis in the MAST Report**. (MAST Report, p. 101, 2250-2254, [“This suggests that overall hydrology (and perhaps overall climate) and its interactions with other environmental drivers has a very strong effect on habitat available to delta smelt spawning and larval rearing. This includes the effect of hydrology on OMR flows and entrainment, but likely also on many of the other habitat attributes shown in the conceptual models presented here (figs. 9-12).”])

- **Comments on MAST Report Figure 44**

Figure 44 is a linear correlation between the SKT index and the previous FMWT Index. This linear correlation is problematic.

First, large abundance values are given undue weight. We are interested in the index ratios between values in all years, not just the big abundance years.

Figure 44 uses a linear correlation between data measured on two different metrics, which can produce misleading results. We are interested in whether SKT Index is directly proportional to the FMWT index (e.g., if FMWT doubles, does SKT double?). The way to learn this answer is to correlate Log SKT versus Log FMWT. We have done so and the result is below. See Figure J. There is still a good correlation. But now you can see that the SKT varies as $FMWT^{0.62}$ or fairly close to the square root of FMWT. This indicates that the FMWT (or less likely the SKT) may be inaccurate and that the true population of delta smelt may have dropped much less than suggested by the FMWT Index. One way to see this effect is to look at the range of the trend line. Log SKT varies from about 1.3 to 2.1 or $SKT_{max}/SKT_{min}=6.3$. But over the same period log FMWT Index goes from 1.2 to 2.5 or $FMWT_{max}/FMWT_{min} = 20$. Both show declines, but the fractional decline is quite different. Thus, if the FMWT were to be linearly related to the SKT, then the lowest values of FMWT during the POD years would need to be approximately tripled.

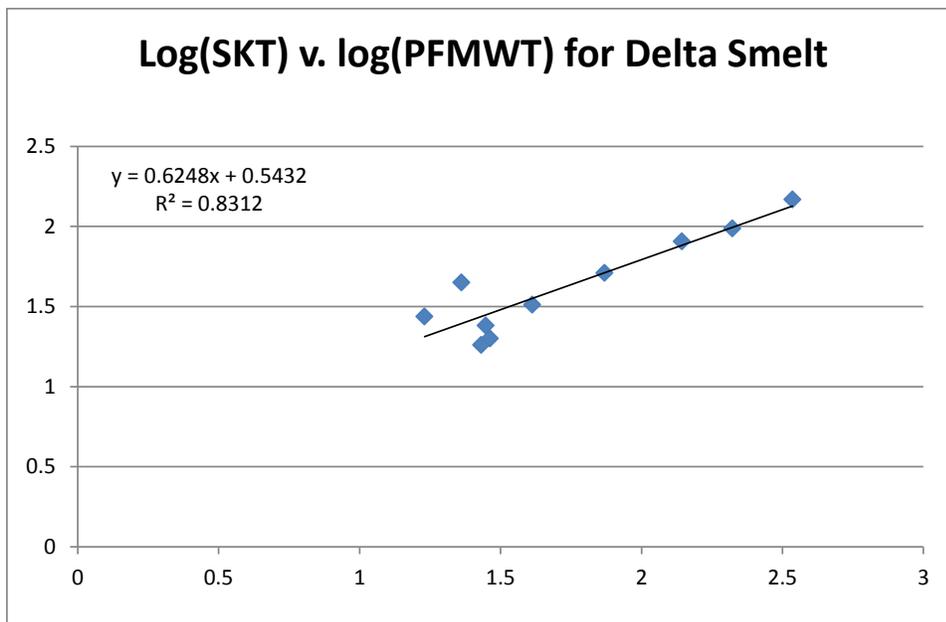


Figure J. Log (SKT) v. log (previous FMWT) for delta smelt.

- **Comment on MAST Report p. 115-116, Table 4**

The MAST Report did not even address the Fall X2 issue, largely deferring to FLaSH. The analysis that was included calculated the volume of habitat based on McWilliams (not Feyrer 2010) to represent simple open water acres within certain salinity ranges for 2005, 2006, 2010 and 2011. The MAST Report conclusion that the data “generally” support the fall X2 theory contained in the BiOp is not sufficiently supported. The use of so few years of data is a violation of generally accepted statistical principles. The problem with this approach can be illustrated by considering an increasing number of years in the analysis. The more years that are considered, the weaker the statistical relationship. See Figures K through M.

Looking at all the years since 1975, there is no relationship between FMWT and Fall X2.

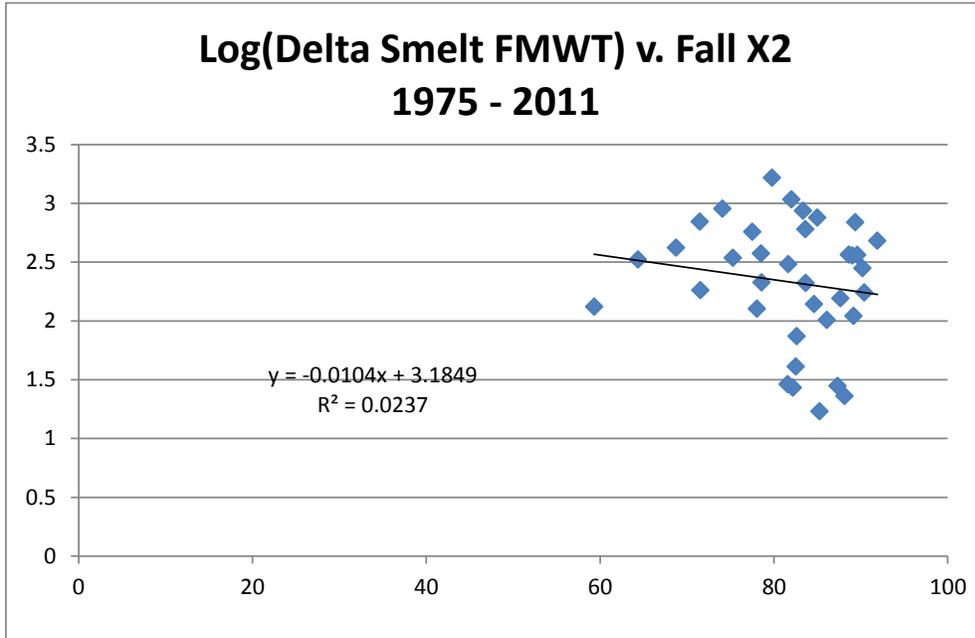


Figure K. Log (Delta smelt FMWT) v. FMWT X2 (1975-2011)

Looking at all the years since 1987, there is no relationship between FMWT and X2

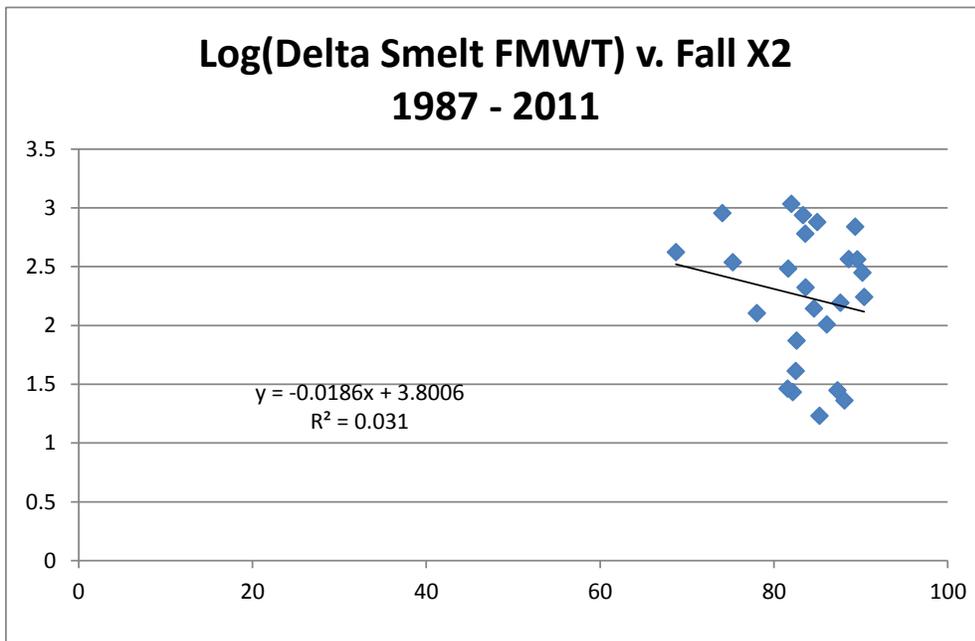


Figure L. Log (Delta smelt FMWT) v. Fall X2 for years (1987-2011)

There is a moderate correlation during the POD years between FMWT and Fall X2 driven entirely by a single datapoint (2011). The only way to generate a strong relationship is to exclude all years except 2005-2011 (making the influence of the single outlier in 2011 more dominant), and such an exclusion of data is not justifiable.

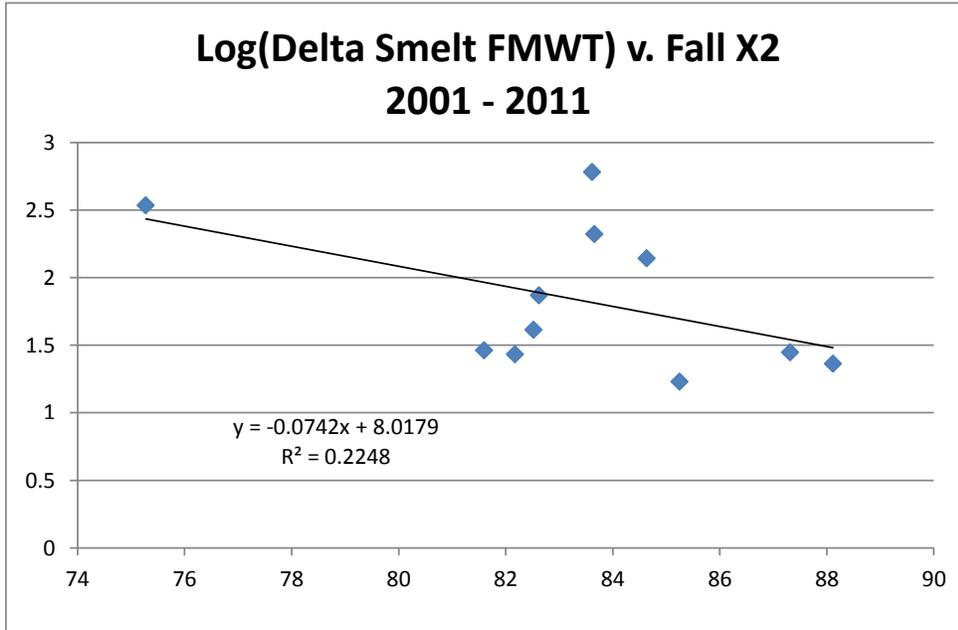


Figure M. Log (Delta smelt FMWT) v. Fall X2 for years (2001-2011)

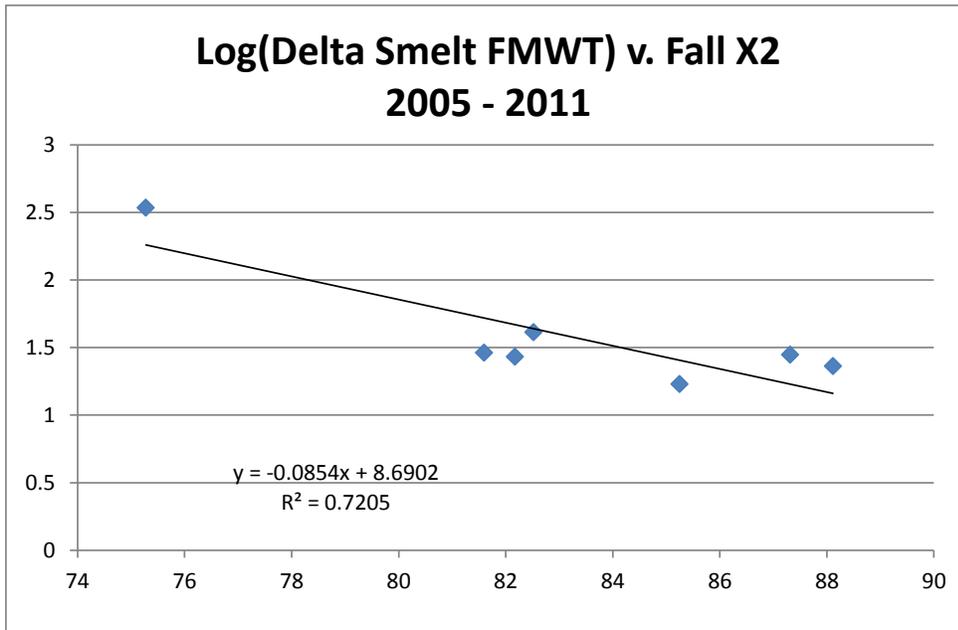


Figure N. Log (Delta smelt FMWT) v. Fall X2 for years 2005-2011.

- **Comment on MAST Report, p. 82, lines 1829-1843**

The MAST Report suggests that the FMWT might be a good surrogate for estimating long-term trends. However, as explained above, while the SKT and the FMWT indices track, the MAST Report fails to acknowledge that the SKT is roughly proportional to the square root of the FMWT index, meaning that if FMWT changes by a factor of 4, then

SKT changes by a factor of 2. If the FMWT changes by a factor of 9, then SKT changes by a factor of 3. As discussed above, there is good reason to think that the FMWT should not be relied upon during low abundance years and thus abundance ratios which use the FMWT Index during the POD years should not be relied upon.

- **Comments on MAST Report, p. 112, lines 2453**

The statement in the MAST Report is that the apparent carrying capacity from STN to FMWT has declined. This statement is partially contradicted elsewhere in the MAST Report, where it states:

Despite this low level, the 2011 adults produced the highest adult abundance observed to date in 2012 [meaning SKT]. This suggests that within the range of adult variability observed in the SKT, adult stock size has not been a limiting factor in subsequent adult recruitment.” MAST Report at p. 93, line 2077-2080.

This statement on page 93 is limited to the SKT years since 2002. The statement is more fully contradicted by looking at 2011 FMWT. The bounce in FMWT from 2010 to 2011 was enormous – a factor of ten – and that was the largest percentage bounce since 1975. Moreover, looking at absolute terms rather than just as a ratio, the value of the FMWT in 2011 was in the same range as FMWT values during earlier periods when conditions were supposedly better. This was impressive considering that the STN value of 2011 was not particularly high. So the idea that carrying capacity has declined is questionable, even if we were to assume that the abundance indices are representative. If potential survey error considerations are included, then the observed shift in the FMWT/STN relationship may be significantly overstated.

- **Comments on MAST Report Figure 18 and p. 39, lines 878-881**

The MAST Report states in reference to the historical X2 position that “The seasonal and interannual variations have become muted, especially in the summer and fall (fig. 18)”. Although this statement has been made elsewhere in the literature, to our knowledge it has not been supported in a rigorous quantitative manner.

Figure 18 is a fails to confirm the statement for the following reasons:

1. The 2001-10 decade is the third driest decade since the beginning of the 20th century – wetter only than the extremely dry decades of the 1920s and 1930s (reported by Hutton to the SWRCB in the 2012 Analytical Tools Workshop, Section 3, pp. 16-34, attached).
2. Unimpaired X2 estimates do not represent reality, as the unimpaired Delta outflow calculation is significantly different than natural Delta outflow conditions (as reported by Hutton to the SWRCB in the 2012 Analytical Tools Workshop, Section 3, pp. 34-57, attached).

3. Even assuming for the sake of argument that unimpaired X2 estimates had analytical value, the comparison should have been made for the same hydrologic period, *i.e.* show unimpaired X2 calculations for the years 2000-2011.
- **Comments on MAST Report p. 49, line 1083; p. 61, line 1362; p. 65, line 1462; p. 65, line 1462; p. 68, line 1534-1535; p. 70, line 1561**

The MAST Report consistently ignores the significant amount of published research by Drs. Glibert, Dugdale, Wilkerson, Parker and Jassby on nutrients, primary productivity and food web structure and function. There is a passing reference but no in-depth discussion of their work. This oversight results in a Report that is incomplete and unbalanced.

- **Comments on MAST Report p. 50, lines 1107-1117**

The MAST Report cites Kimmerer 2008 but fails to also mention the significant error bars acknowledged by Kimmerer, improperly citing the 0-50% range as if these differences occur in different years. The MAST Report goes on to cite Kimmerer 2008 as supporting a finding that entrainment has a population level effect, while Kimmerer specifically stated that he did not find a population level effect.

The MAST Report cites Maunder and Deriso as having found that high entrainment can affect subsequent generations. The Maunder and Deriso best fit model did not find that entrainment was significant. There was a lesser model that identified entrainment as having a marginal effect; but when the data in the model was updated to 2010 (from 2006), the model no longer identified entrainment as even having a marginal effect.

Thomson et al. (2010) is also referenced as supporting the notion that high entrainment losses can adversely affect subsequent populations. In fact, entrainment was not one of the covariates tested by Thomson et al. (2010) and the word “entrainment” does not even appear in the body of the manuscript.

- **Comment on MAST Report p. 84, lines 1880-1884**

The MAST Report argues that delta smelt are density independent due to low abundance. The Report cites Kimmerer 2011 as evidence that any source of mortality will accumulate year-by-year. Kimmerer did not show that such an impact is accumulating, he merely made the theoretical argument that such accumulation is possible.

Dr. Richard Deriso analyzed this statement regarding accumulating impact, and it is his position that within standard fish stock-recruitment models a new source of mortality will merely lead to a new steady-state population that is slightly lower than before. Specifically, Dr. Deriso's⁶ view is that:

⁶ Dr. Richard Deriso, Personal communication.

If the population is at a low level of abundance then with conventional stock production models, such as the Ricker recruitment model, then it is true that substantive compensatory density-dependence is unlikely to be occurring. However it is also true that natural survival is maximized at a low level of abundance. Therefore the population would not increase only if the impact mortality is roughly greater than the species maximum intrinsic rate of growth. Furthermore in impact analysis the long-term equilibrium reduction in a population due to a constant annual mortality (such as through entrainment) is dependent on the maximum intrinsic rate of growth. For example, in a Ricker model, $B(t+1) = B(t)(1-F)\exp(a-b*B(t))$, the percent reduction in equilibrium abundance due to a given constant annual mortality “F” is equal to $-\ln(1-F)/a$ (Lawson and Hilborn 1985).. The parameter “a” is the maximum intrinsic rate of growth. Note that the long-term equilibrium abundance does not depend on initial population size. (Lawson, T.A. and R. Hilborn. 1985. Equilibrium yields and yield isopleths from a general age-structured model of harvested populations. *Can. J. Fish. Aquat. Sci.* 42: 1766-1771.)

It is not clear at present whether or not delta smelt abundance is low, at least based on the high FMWT index for 2011. Needless to say some caution should be exercised in basing a strong conclusion on a single year’s index.

- **Comments on MAST Report, p. 41, lines 912-916**

The MAST Report describes the hypothesis by Feyrer et al. (2007 and 2011) that reductions in habitat area may be related to reductions in delta smelt abundance. To balance this discussion, the report should also describe the finding by Kimmerer *et al.* (2009) that delta smelt abundance does not appear to be related to habitat volume

- **Comments on MAST Report, p. 41, lines 921**

The position of the LSZ also affects ammonium concentrations, which may in turn affect phytoplankton and zooplankton biomass and species composition (Dugdale *et al.* 2007⁷; Glibert *et al.* 2011⁸.)

- **Comments on MAST Report, p. 42, lines 935-938**

⁷ Dugdale, R.C., F. P. Wilkerson, V. E. Hogue and A. Marchi. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuarine, Coastal and Shelf Science* 73: 17-29

⁸ Glibert, P.M., Fullerton, D., Burkholder, J.M. Cornwell, J.C., Kana, T.M. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco Estuary and Comparative Systems. *Reviews in Fisheries Science*, 19(4): 1-60.

The Report states that there is no evidence to support the effect of low turbidity on survival, growth, and reproduction. However, studies by Linberg and Baskerville-Bridges have found low turbidity effects feeding success of larval delta smelt.

- **Comments on MAST Report, p. 43, line 950**

The Report says there are two main sources of turbidity in the upper estuary. A third source of turbidity is plankton concentration. A discussion of this third source should be included.

- **Comments on MAST Report, p. 49, lines 1101-1103**

Salvage is described as occurring nearly year-round in the beginning of the time series and now only from December to June. This observation seems to merit additional inquiry. For example, does this observation suggest that delta smelt may have occupied freshwater regions year-round in the past, as is now being observed in Cache Slough region? When did this occurrence change? Were delta smelt salvaged at approximately the same quantities year-round, or was there a peak that corresponds to the period of time when we observe salvage now?

- **Comments on MAST Report, p. 50, lines 1124-1127**

Castillo *et al.* (2012) is described without also describing the limitations of that study's design, such as water temperatures, location of releases, and pumping rates at the time of the study.

- **Comments on MAST Report, p. 84, lines 1869-1871**

The Report describes years with bigger females and higher spawning stock size as having better reproductive potential. Years with suitable spawning temperatures over longer periods of time should also be considered as having greater reproductive potential.

- **Comments on MAST Report, p. 87, lines 1936-1939**

The Report concludes that hydrology and exports interact to influence entrainment risk for adult delta smelt (Hypothesis 1). While there is evidence to support this, it is not presented in the discussion for this hypothesis beginning on p. 85. The information presented in pages 85-87 under Hypothesis 1 does not support his conclusion.

- **Comments on MAST Report, Figure 52, p. 90, lines 2005-2007**

The Report concludes that Hypothesis 4 is partially supported seemingly based on an observation of growth in 2011 being higher than in the comparison of years. However, Figure 52 does not show any difference in growth between 2011 and 2005 (a wet year and a dry year), and based on the variability, it is not apparent that there is a significant difference between any of the years.

- **Comments on MAST Report, p. 105, lines 2311-2313**

It should be noted that high water temperatures can also increase susceptibility to disease and to some contaminants.

Appendix 4

Question 6: What other significant improvements, if any, might be made in the report?

Three additional areas of discussion within the Report would significantly improve the report: 1.) survey error, 2.) the role of nutrients, and 3.) the role of contaminants.

Survey Error:

The MAST Report should acknowledge that the existing surveys are imperfect and include a hypothesis to the conceptual model that investigates the role of survey error. At the very least, the MAST Report should acknowledge that before extensive data analysis can be undertaken to determine likely factors affecting species abundance, there needs to be an investigation into the nature and extent of survey error, and that error needs to be corrected in the data (to the extent possible) before extensive data analysis is undertaken. We understand that the existing data is the best that we have and that we have all used that data for decades in various analyses in attempts to tease out potential factors affecting species abundance, but it has become increasingly clear that the surveys may not be reliable, particularly for teasing out the effects of specific variables on species responses, but also for assessing trends over time to the extent that the influence of these survey errors may have changed over time. The unreliable nature of the existing data makes results of data analyses difficult to interpret and the resulting confidences on the results are low.

There is good reason to believe our existing delta smelt surveys are not representative of smelt abundance or distribution. For example, Feyrer et al (2013) observed in their “smelt-cam” research that delta smelt change their distribution according to the tidal cycles in apparent attempts to control their position. On the ebb tide delta smelt were observed moving to the sides of the channel. On the flood tide delta smelt were caught in the middle of the channel. These findings are consistent with previous observations by Bill Bennett and Jon Bureau. This is significant as the surveys only sample in the middle of the channels and there is no established protocol for only sampling on the same tidal cycle each survey. Other evidence of tidal cycle sampling error can be observed in Figures U through BB.

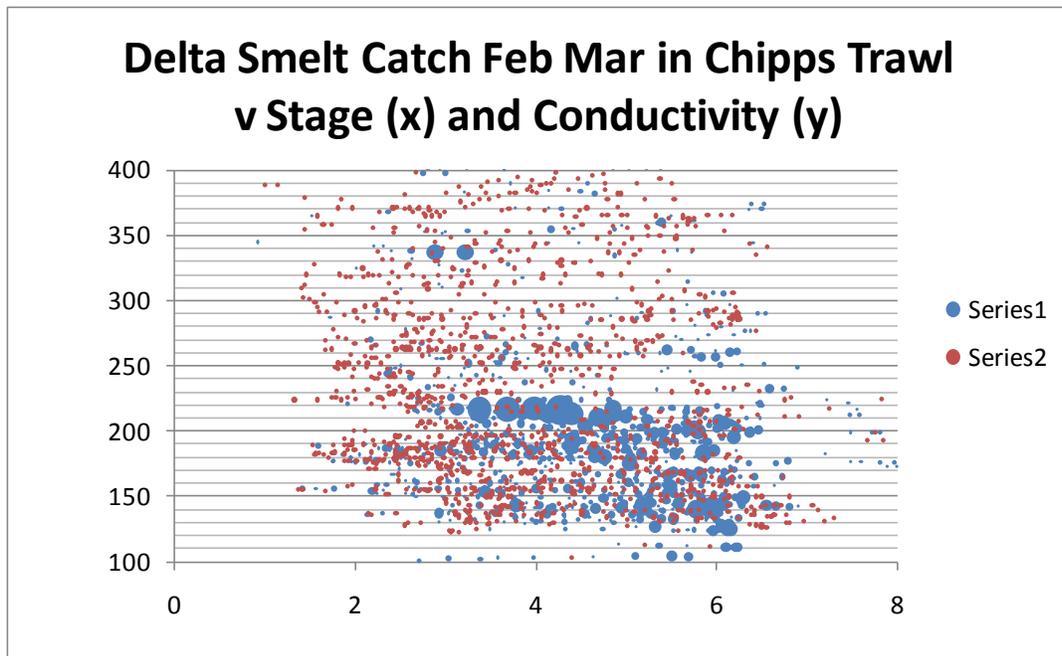


Figure U. Delta smelt catch (February-March) in Chipps Island v. Stage (x) and Conductivity (y)

Figure U is from the Chipps Island Trawl where stage is drawn from the Mallard Slough dataset rather than from DSM (data compiled by Dr. Ken Newman). Only the conductivity range 100 – 400 EC is shown. There are a few interesting things to observe in Figure U. There are frequent catches of smelt when conductivity is below about 250. Catches above 250 EC are rare. Why would this be? Are delta smelt absent from the Chipps area when flows are somewhat reduced such that salinity is in the 250 – 400 EC range? Or, are delta smelt invisible to the nets? Second, note that the stage at which delta smelt are caught becomes increasingly limited to the highest stages as conductivity falls (i.e., flow increases). Thus, as flows increase, the fraction of time that delta smelt are visible (caught in the surveys) decreases. Given that FMWT and other surveys are not always taken on the same phase of tide at different stations and in different years, the expected catch probably shifts dramatically and could impact estimated distributions and abundance. Unless this survey error is accounted for, it will be difficult to have confidence in the distribution and abundance data.

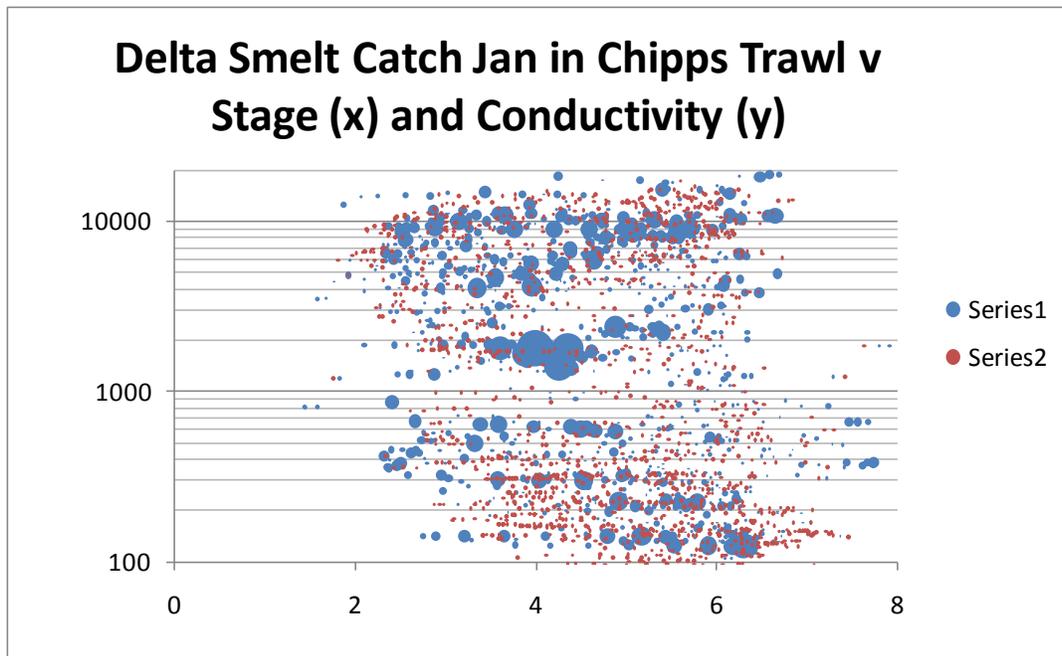


Figure V. Delta smelt catch in January in the Chipps Trawl v. Stage (x) and Conductivity (y)

Figure V is the same graph as Figure U but for January. Note the restriction in stage at the lowest salinities as in the previous figure. Note that from EC of about 2000 to 10000 delta smelt appear to be present at all stages of the tide. Could this phenomenon be responsible for the peak in delta smelt presence/absence around X2 identified by Feyrer? That is, could the supposed peak in smelt presence really be an artifact of surfing behavior?

There are other potential survey biases as well. There is evidence of a wind bias in Figure W. During months when turbidity could be quite variable due to changing winds, FMWT catch is heavily influenced by wind. The reason for the change in catch is likely due to wind generated turbidity which increases catch efficiency. Figure W.

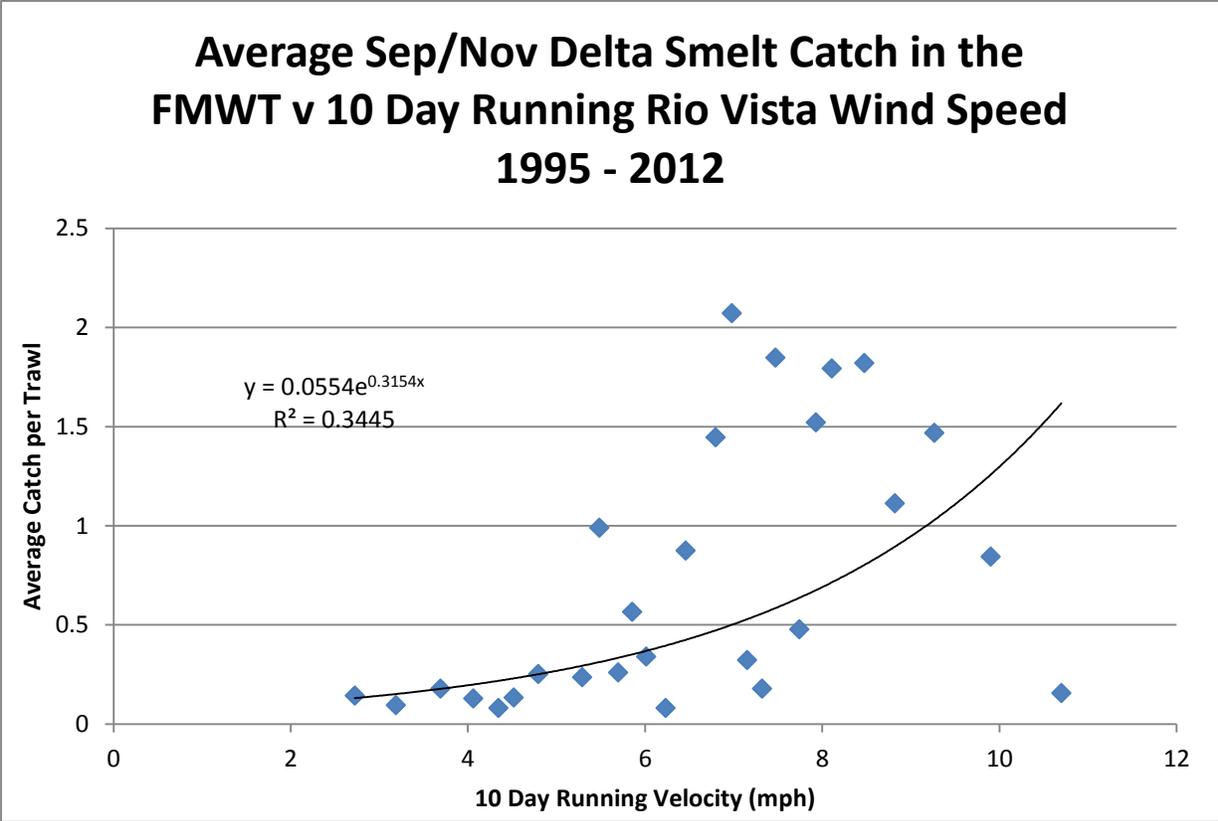


Figure W. Average September/November delta smelt catch CPUE in the FMWT v. 10 day running average Rio Vista wind speed.

There is evidence of a time of day bias in Figure X. A strong time of day signal is observable in this dataset. The majority of the normalized catch occurs before 9:00 am in the morning between the conductivity range of about 300-9000 EC. Figure X.

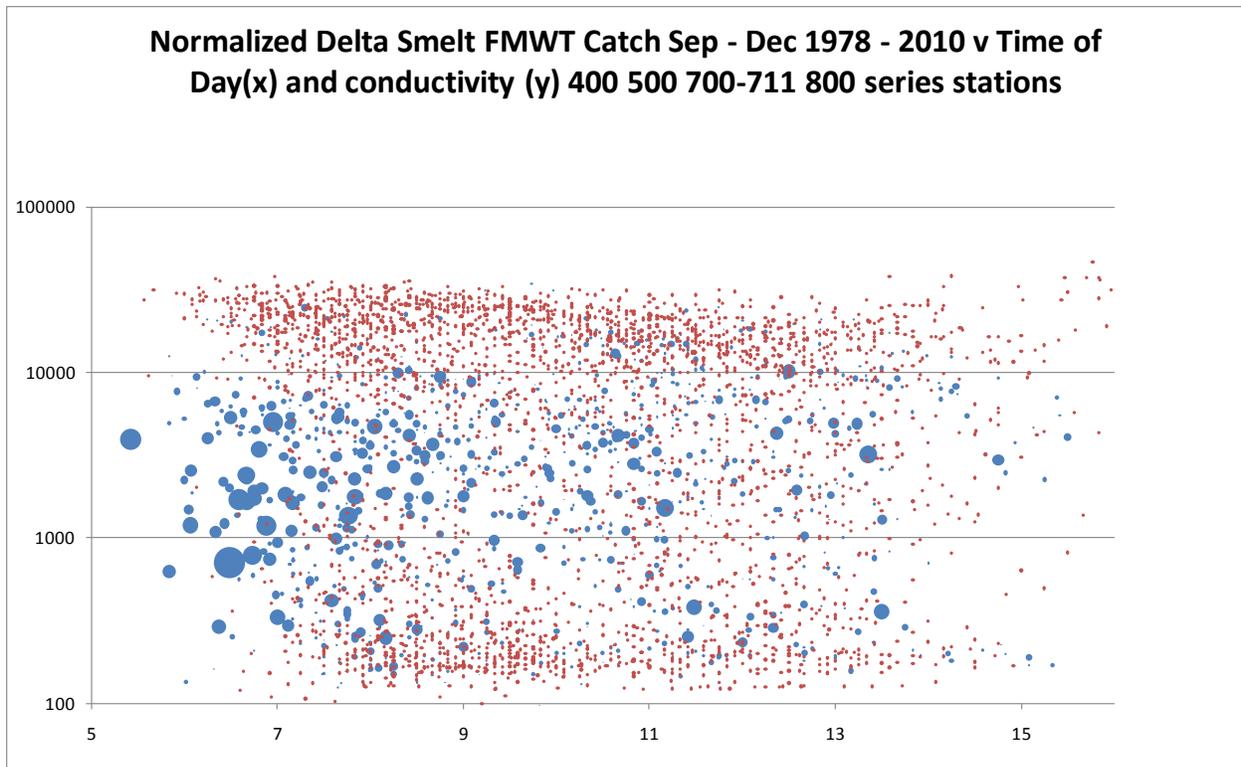


Figure X. Normalized delta smelt FMWT catch September-December 1978-2010 v. time of day(x) and conductivity (y), stations series 400, 500, 700-711, and 800.

Longitude and time of day (Figure Y) arguably give an even tighter fit to the FMWT data than does salinity and time of day. Most catch occurs before 9:00 between -121.7 and -121.8 longitude (*i.e.*, near the confluence). Catch at this longitude is sparse after 9:00. There are few, if any, samples in the early morning for the longitude range -121.9 to -122.1, meaning that the survey might be missing the opportunity for large catches in much of Suisun Bay. Additional support for the hypothesis that delta smelt survey catch is subject to time of day survey error comes from the salvage dataset. Salvage is recorded day and night and so differences in smelt vulnerability to catch might be revealed by salvage patterns. Figure Z shows average salvage densities for juvenile delta smelt, May-July 1993-2013 versus time of day. Expected salvage densities vary by a factor of 5 from day to night. FMWT sampling is not standardized by time of day. Sampling began before dawn during the 1990s. The earliest sampling times shifted to several hours later in the day at the same time the POD occurred. This could account for at least some of the declines in the delta smelt FMWT index. Thus, it is no surprise that average time of day of the FMWT trawl is one of the most powerful correlates to the FMWT index since time began to be recorded in 1978. See Figure AA.

Many stations rarely, if ever, are sampled early in the day because those stations occur late in the sampling order for the boats. If sampling occurred earlier in the day at these stations, catch might be higher. Thus, the protocol for which stations are sampled first in the day and which are sampled later in the day could be influencing apparent distributions of delta smelt. For example, the stations near the bottom of Sherman Island are generally sampled early in the day because they are near to where the trawling boat is docked.

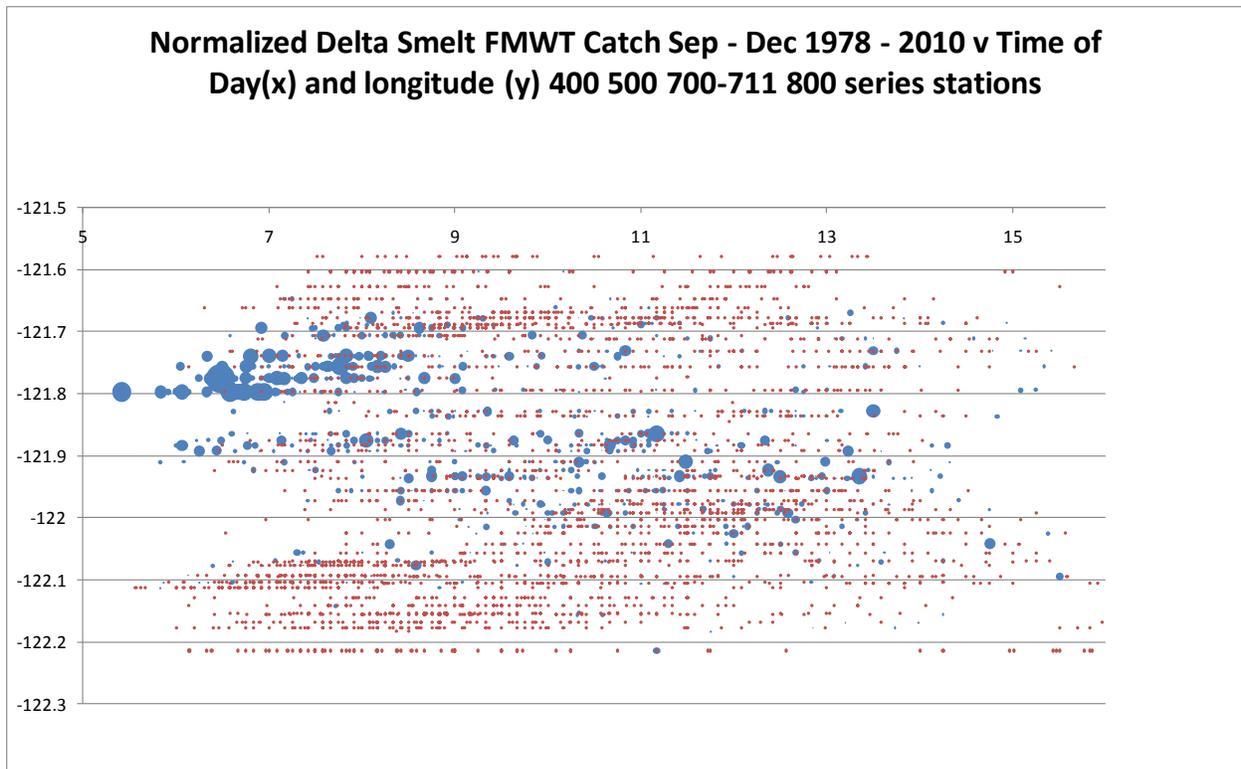


Figure Y. Normalized delta smelt FMWT catch, September through December (1978-2010) v. Time of day(x) and longitude (y), stations series 400, 500, 700-711 and 800.

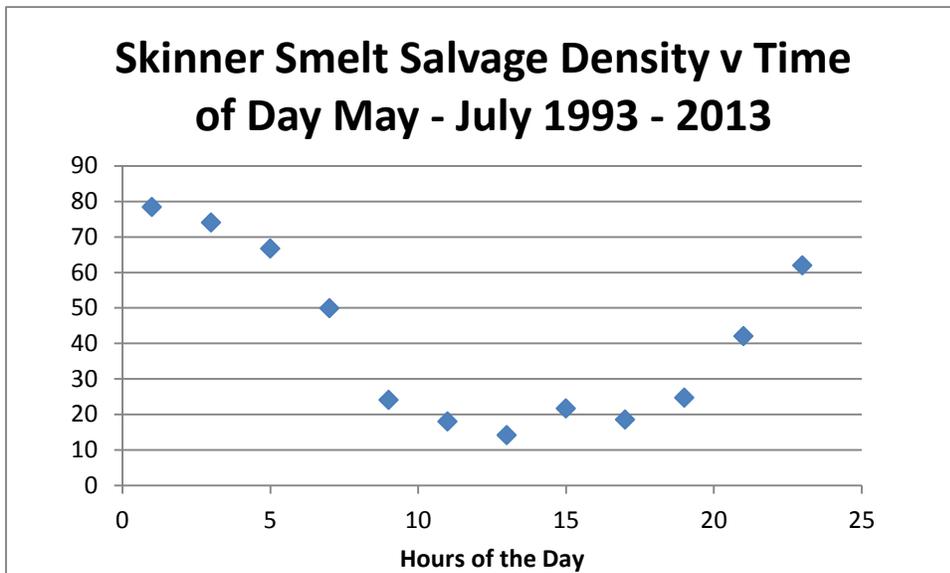


Figure Z. Average delta smelt salvage density at Skinner computed as $1,000,000 \times \text{salvage/test/pumping rate}$ May-July 1993-2013.

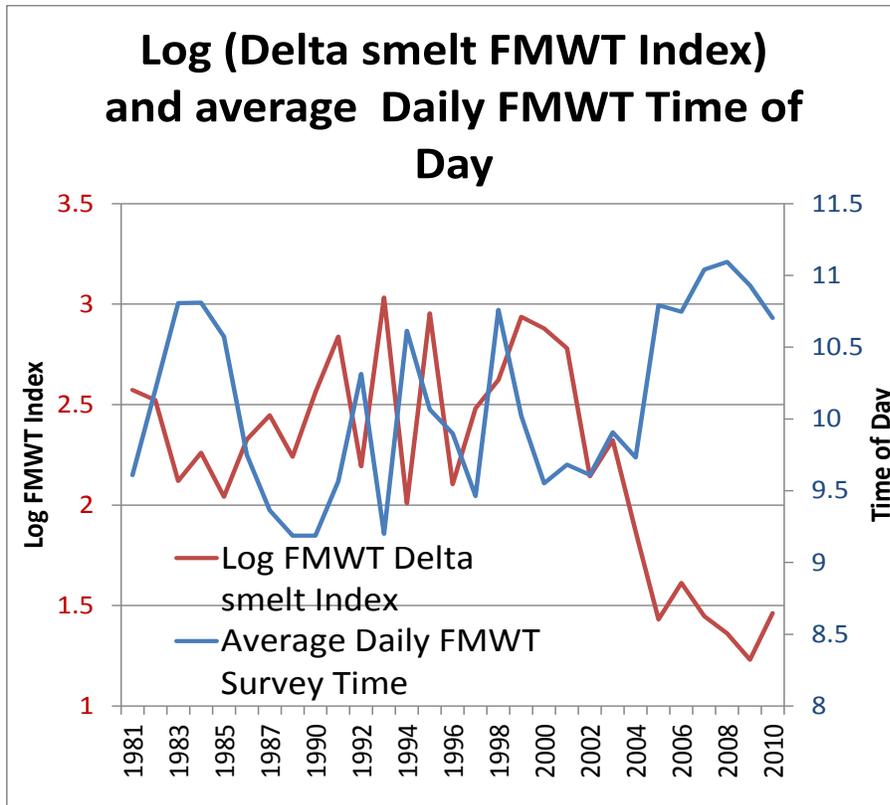


Figure AA. Log delta smelt FMWT Index v. average daily time of day in the FMWT.

There is also evidence of a geographic bias related to water depth in the FMWT. See Figure T. The FMWT surveys sample heavily in the deep water channels between 25 and 40 feet deep. There are very few measurements in water shallower than 25 feet deep. However, it is apparent from the data that there could be substantial catch at shallower depths. Therefore, the FMWT surveys give us little information about what is happening in water below 25 feet deep, which is an area that covers the majority of Suisun Bay, Grizzly Bay and Honker Bay.

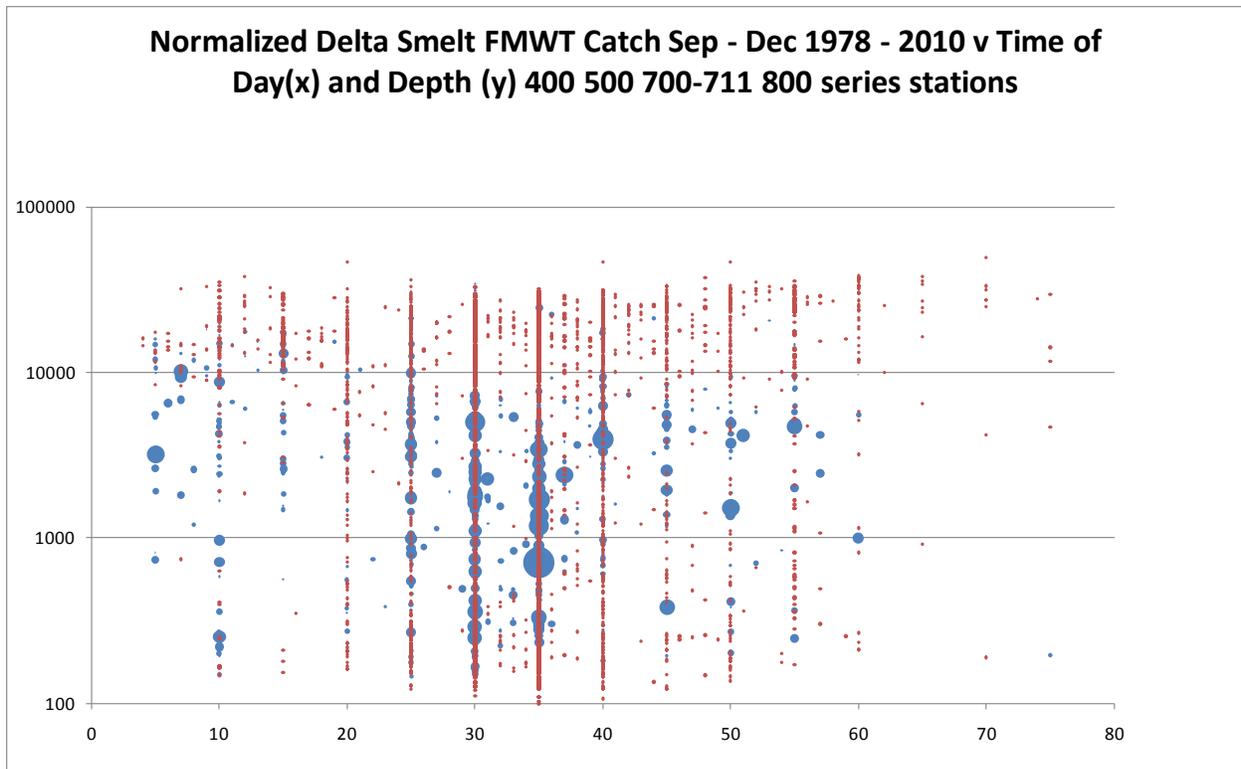


Figure BB. Normalized delta smelt FMWT catch, September-December (1978-2010) v. Time of Day (x) and depth (y), stations series 400, 500, 700-711, and 800.

Role of Nutrients:

The Report would be significantly improved by additional discussion and analysis of the role of nutrients in SFE structure and function as well as the differences in nutrients during the four years analyzed in this report. The SWC would be pleased to provide additional information to inform this discussion and attach a technical memorandum, “Nutrient Science Summary” as a start.

Role of Contaminants:

The discussion of contaminants could also be improved with additional discussion and analysis. For example, on MAST Report, p. 38, line 840, it should also state that higher water temperatures can also affect fish vulnerability to disease and contaminants. On MAST Report, p. 57, lines 1265-1266, it should acknowledge that while the concentrations of individual pesticides were lower than would be expected to cause acute mortality, the effect of pesticide mixtures is unknown. The studies cited all detected multiple pesticides in every sample analyzed. The interaction between pesticides should be acknowledged. It should also be acknowledged that contaminants can also affect predator-prey interactions by altering prey behavior (Brooks *et al.* 2009).¹ Finally, there is additional, newer information on pesticide occurrence and the effect of pesticide mixtures on the food web that can and should be included.

¹ Brooks, A.C., Gaskell, P.N., Maltby, L.L. 2009. Sublethal effects and predator-prey interactions: implications for ecological risk assessment. *Environmental Toxicology and Chemistry*, Vol. 28, No. 11. Pp. 2449-2457.

Eastward migration or marsh-ward dispersal: understanding seasonal movements by delta smelt

Dennis D. Murphy

Biology Department
University of Nevada
Reno, Nevada 89557

Scott A. Hamilton

Center for California Water Policy and Management
1017 L Street, Suite 474
Sacramento, CA 95814

ABSTRACT

Differing and confounding understandings of the seasonal movements of the delta smelt in the San Francisco estuary persist nearly two decades after its listing as threatened under the federal and state Endangered Species Acts. The U.S. Fish and Wildlife Service and Bureau of Reclamation have characterized the delta smelt as a species that migrates extensive distances from Suisun Bay and the confluence of the Sacramento and San Joaquin rivers in the fall and winter, eastward and upstream to the central and east Delta to spawn, with the next generation returning to downstream rearing areas in the following spring. This description of inter-seasonal movements by delta smelt stands in contrast to findings drawn from previous studies, which describe movements by pre-spawner delta smelt from open waters in bays and channels to adjacent marshlands and freshwater inlets. In an effort to resolve this disagreement over the movements of delta smelt, we use publically available data on its distribution drawn from trawl surveys to generate maps from which we infer seasonal patterns of dispersal. In the fall, prior to spawning, delta smelt are most abundant in Suisun Bay, the Sacramento and San Joaquin rivers confluence, the lower Sacramento River, and the Cache Slough complex. By March and April, the period of peak detection of spawning adults, relative densities in Suisun Bay and the rivers confluence have diminished in favor of higher concentrations of delta smelt in Montezuma Slough and the Cache Slough complex. A relatively small percentage of fish are observed in areas of the Sacramento River above Cache Slough. We conclude that inter-seasonal dispersal of delta smelt is more circumscribed than has been previously reported. This conclusion has profound implications for efforts to conserve delta smelt. Our findings support a conservation strategy for delta smelt that focuses on habitat restoration and management efforts for tidal marsh and other wetlands in north Delta shoreline areas directly adjacent to open waters that have been documented to support higher concentrations of the fish.

Keywords: delta smelt, distribution, dispersal, spawning migration, inter-seasonal movement.

Introduction

From assessments of gene flow to projections of metapopulation dynamics, virtually every essential aspect of conservation planning calls for an understanding of patterns of movement by targeted at-risk species. And, while a rough appreciation of dispersal exists for most protected species, the once-abundant delta smelt (*Hypomesus transpacificus*), which is endemic to central California's San Francisco estuary, is a species for which an absence of data on dispersal has fed controversy over appropriate conservation actions that are needed to recover the species and restore its habitats, and allocation of the resources required for its protection. Because the fish is small, nearly transparent, and preternaturally fragile, the movements of delta smelt have proven exceptionally difficult to track in the turbid waters of the estuary. So elusive is the fish throughout its annual life cycle, it actually has not been observed spawning in nature (Moyle 2002, Bennett 2005); and, while its distributional range has recently been resolved to the extent practicable using available surveys (Merz et al. 2011), its dispersal patterns within that range remain in doubt (but see Bennett 2005). Data from a series of trawl surveys in the San Francisco estuary suggest that different delta smelt life stages use different areas of the estuary's water bodies and channels; however, since delta smelt are not directly observed in those habitats and cannot readily be marked or tagged, the details of delta smelt movements have been the subjects of surmise (Sommer et al. 2011).

Two decades after the delta smelt received protection as a threatened species under the federal Endangered Species Act, uncertainties persist regarding distribution and dispersal across the estuary during its short, annual life cycle. But, while individual survey samples that capture delta smelt offer limited direct information regarding dispersal by the species, when the multiple trawler-based surveys in the San Francisco estuary that record the fish throughout its annual life cycle are viewed in sequence, evidence of its continuously shifting overall distribution becomes apparent. And, although the movements of individual delta smelt remain obscure, geographic patterns of its presence and absence, and its temporally and spatially shifting densities, can be gleaned from trawl surveys and used to infer inter-seasonal patterns in its movements.

Despite publically available long-term data sets on the distribution of the species, two dramatically differing perspectives have emerged in the literature and in federal planning documents and presentations regarding the movements of adult delta smelt prior to spawning. One perspective is provided by Bennett (2005), who noted that in "the fall, delta smelt gradually begin a diffuse migration landward to the freshwater portion of the Delta, and during wetter years to the channels and sloughs in Suisun Marsh and the lower Napa River." Bennett's description is consistent with that articulated by Moyle (2002 and Moyle et al. 1992), reflecting previous observations from focused surveys reported by Radtke (1966), Wang (1986, 1991), and Wang and Brown (1993). The narrative depiction that can be drawn from those studies is that of dispersal in multiple directions by pre-spawner

delta smelt, from the bays, embayments, and channels of the estuary's low-salinity zone, to adjacent marshlands and freshwater inlets that support spawning, with juvenile fish from the next generation distributing themselves into adjacent open waters where they feed and grow for several months, then repeat the cycle of dispersal toward marshland and freshwater spawning locations.

The other perspective on delta smelt movement describes a uniform, upstream migration of delta smelt from open waters in western portions of the Delta's low-salinity zone toward its eastern freshwater limits. Department of the Interior agencies have described large-scale, seasonal, directional movement by delta smelt in a pair of maps; the first (Figure 1a) was presented by the U.S. Fish and Wildlife Service in a presentation to the National Research Council's Committee on Sustainable Water and Environmental Management in the California Bay-Delta (USFWS 2010). It illustrates a seasonally bimodal distribution of delta smelt in which the fish feeds and matures in the western Delta from the early spring to the late autumn and early winter, at which time pre-spawning adults migrate en masse east to a distinct eastern distribution for spawning. The next generation returns to previously occupied west estuary waters to repeat the cycle. The second map (Figure 1b) was offered in a draft document describing an adaptive management plan that was required to accompany the prescribed management actions in Service's biological opinion (USBR 2012). It shows an eastward shift in the distribution of delta smelt, but from a broader mid-year footprint in the western portion of the Delta toward a partially overlapping, more-eastern distribution just prior to spawning, followed by a return to the more western distribution by the next generation. Both maps were accompanied by discussions that described those seasonal shifts in distribution as migration events by spawning delta smelt. Combined these two maps can be viewed as a conceptual model of the distribution and migration of delta smelt, the validity of which can be assessed using data from multiple trawler-based surveys in the estuary.

Here we use state agency-generated survey data to produce maps of the distribution of delta smelt across seasons and to obtain an understanding of where delta smelt are most commonly found during each of their several recognizable life stages, both in an effort to determine which, if either, perspective on delta smelt dispersal is consistent with available data. By comparing the locations of season- and life-stage specific occurrence polygons, which include 95% of delta smelt sampled from five readily available fish surveys, we draw parsimonious inferences concerning inter-seasonal movements by the fish. We contrast our findings with those presented in a recent assessment of the spawning migration of delta smelt in the upper San Francisco estuary by Sommer et al. (2011).

We consider the relevance of information on delta smelt distribution and dispersal to the multiple conservation planning efforts in the Delta. Resource managers at the Department of the Interior have utilized and are utilizing the first perspective to inform their ongoing conservation planning efforts targeting the delta smelt (USFWS 2008, USBR 2012, BDCP 2013). Comprehensive planning includes recovery

actions that directly target delta smelt, restoration efforts that seek to restore essential components of its diminished habitats, and management of Delta through flows, which have been controversially identified as a proximate cause in the decline of the listed species. Implications of the two dispersal perspectives for the types, locations, and prioritization of species recovery actions and habitat restoration activities are profound. The more localized, marsh-ward spawning dispersal phenomenon indicates the need for focused conservation actions in sub-regional context. In contrast, the long-distance, migration phenomenon would expose delta smelt to distinct suites of environmental stressors at either end of a either end of its putative migratory path, and a gauntlet of impacts during long distance movement from one geographic limit of its west-to-east range to the other, all of which presumably need address to realize species recovery.

We attempt to discern the validity of the federal agencies' conceptual model by addressing three de facto hypotheses that are implicit in the geographic details of their maps:

- (1) Directional migration by delta smelt occurs in the late autumn and early winter from western and central portions of the estuary to areas in the eastern estuary that support spawning.
- (2) In migrating seasonally to areas of the eastern Delta, delta smelt effectively vacate Suisun Bay and Suisun Marsh and do not spawn there.
- (3) After spawning occurs, sub-juvenile delta smelt that make up the next generation are predominantly distributed across the central Delta.

We rely on agency-generated, life-stage-specific survey data on delta smelt to test these hypotheses and to draw inferences regarding the spatial distribution of delta smelt and likely patterns of its dispersal. We also consider how the loosely applied nomenclature of dispersal and the generous application of the term "migration" to the many manifestations of animal movement have combined to contribute to a confused narrative regarding the seasonal movements of delta smelt.

Methods

Data Sources and Treatment

Since it is not possible to track delta smelt directly, inferences regarding its inter-seasonal movements require an assessment of the distribution of the fish at each of its life stages. The California Department of Fish and Game carries out multiple surveys of fishes in the San Francisco estuary, returns from which include delta smelt in temporal samples that span the fish's life cycle. Surveys include the 20 mm Survey, Summer Tow-net Survey (STN), Fall Midwater Trawl (FMWT), and Spring Kodiak Survey, which sample extensive, partially overlapping areas of the estuary (within the area in Figure 2). Additionally, USFWS conducts Beach Seine surveys in widely separated areas in the Delta. The methods for those surveys have been documented previously (see Moyle et al. 1992, USFWS 2004, Bennett 2005); the

varying strengths and weaknesses of several of these surveys as population assessment tools for delta smelt have been discussed in detail by Bennett (2005). Each monitoring program survey effort is conducted during a different seasonal (time) period, with a different sampling frequency (monthly or bi-weekly), and at a varying number of stations (30-113 stations). By employing different gear and tools during different time periods, each survey effort serves to sample delta smelt of different sizes and during different life stages. It is important to note that the first four of the aforementioned ongoing surveys largely (but not exclusively) sample fishes from the open waters of the estuary, including its bays and channel midlines. Accordingly, throughout its range, delta smelt move outside of the survey stations to spawn, making available survey returns less than optimal for addressing delta smelt movements to access the shallow areas and freshwater inlets that all observers agree host spawning by the species.

Drawing from discussions of the life history of delta smelt by Moyle (2002) and Bennett (2005), we differentiated five separate delta smelt life stages -- larvae, sub-juveniles, juveniles, sub-adults, and mature adults (Table 1). We chose a 15-mm body length to differentiate between larvae and sub-juveniles, because at 16-18 mm delta smelt exhibit more developed fin structure and their swim bladders are filled, making them more mobile within the water column (Moyle 2002). We used 30-mm as the length threshold between sub-juveniles and juveniles, because this size is associated with a change in observed feeding regime (Moyle 2002). We chose 55-mm as the length that differentiates between juveniles and sub-adults/mature adults, because delta smelt growth demonstrably slows between 55 and 70 mm, presumably because most of their available energy is channeled toward gonadal development (Erkkila et al. 1950, Radtke 1966). Because the state of maturation of individual delta smelt is reported in the Spring Kodiak Trawl, we used reproductive stage to (further) subdivide mature adults into pre-spawners and spawners. Delta smelt in reproductive stages 1 to 3 for females, and stages 1 to 4 for males, were classified as pre-spawning adults; reproductive stage 4 in females and stage 5 in males were classified as spawning adults (J. Adib-Samii, CDFG, pers. comm.).

Although survey data are available for juvenile and adult delta smelt from the FMWT survey back to 1967, here we present survey results from 1987 onward in our comparisons of life-stage distributions, concordant with the introduction to the estuary of the Asian clam (*Potamocorbula amurensis*), which is believed to be responsible for major changes in the delta food web (Alpine and Cloern 1992, Greene et al. 2011, Nichols et al 1990, Winder and Jassby 2011). The 20-mm (tow-net) survey was first conducted in 1995, and was intended to provide data on larval, sub-juvenile, and juvenile delta smelt. Data from the Spring Kodiak trawl are available from 2002. We have not used data accrued from various supplemental sampling efforts that have recorded delta smelt, because such surveys were conducted for special purposes and were not necessarily consistent with programmatic protocols (R. Baxter, CDFG, pers. comm.). To avoid introducing anomalies that might be caused by the addition of new stations to established survey frames, when using data from any of the monitoring programs we only

included sampling stations that were sampled consistently (that is, stations that were sampled in at least 90% of the years).

Distribution by Life Stage

We calculated the average CPUE of delta smelt for each life stage and station for all years by dividing the summed catches C of delta smelt for each life stage l , station s , and time period p in year y by the volume of water in cubic meters V that was sampled for each region and year, then multiplying by 10,000 to determine the catch per 10,000 m³ for each life stage, region, and year:

$$[1] \quad \text{CPUE}_{lspy} = \Sigma C_{lspy} / \Sigma V_{spy} \cdot 10000.$$

Then, the percentage of delta smelt observed at each station in each sampling period was calculated by dividing the result from equation [1] by the total across all stations for each pertinent period in each year (see Table 1). Finally, the average annual percentage of delta smelt for each life stage observed at each station was calculated as a simple average over all years.

While recognizing that the gear employed to sample the estuary's fishes varies in terms of catch efficiency, and that catch efficiency varies both between monitoring programs and within samples of each monitoring program (depending on a variety of factors, including the size of individual delta smelt), we did not attempt to adjust the results reported here for catch efficiency. As a result, we draw no conclusions regarding the census number of delta smelt, which can vary substantially in returns from different monitoring programs, and discordantly between life stages from within a individual monitoring program.

Our treatment of delta smelt catch data was limited to the observed distribution, rather than informed by population estimates. The latter would have required estimates of the volumes of the targeted bodies of water and reliance on the assumption that samples are representative of the density of fish throughout the water bodies. The validity of such an assumption may be questionable in a variety of circumstances, particularly when using Beach Seine data, since the demarcation between "beach habitat" and "open-water habitat" is inherently arbitrary.

To depict spatially the distribution of each life stage across all years sampled, we identified the fewest stations that accounted for 90% of the sampled fish, showing these as dark circles around the relevant station, and the next 9% as light circles (for example, Figure 3a). Stations that accounted for less than 0.2% of the observed distribution were considered *de minimis* and not depicted. The extent of the range of each survey is shown as a solid surrounding line. Areas without shading within the surrounding line support very few delta smelt.

To test the first hypothesis -- that there is a unidirectional movement by delta smelt toward eastern spawning areas in the Delta -- we looked for a net increase in the

percentage of fish east of the rivers' confluence (east of stations 703 and 804), from the sub-adult life stage in September and October to the pre-spawning life stage in the subsequent January to May. For this hypothesis (and the second), we considered data from pre-spawning adults rather than spawning adults, having observed that the number of spawning adults sampled was far fewer (80% less) than the number of pre-spawning adults; spawning adults presumably move out of deeper, open waters where the monitoring stations are largely located. We tested the difference between the numbers of delta smelt in the two geographic areas using a one-tailed t-test, since the federal agencies presume the movement is unidirectional to the east.

To test the second hypothesis -- that delta smelt vacate the Suisun bay and marsh complex to spawn in eastern portions of the Delta -- we tested whether the percentage of pre-spawning adults in the area of the rivers confluence and further west (as identified above) were significantly different from zero. We used a one-tailed test since the percentage could not be negative.

To test the third hypothesis -- that sub-juvenile delta smelt are distributed predominantly across the central Delta in the spring -- we compared the percentage of sub-juveniles in the central delta with the percentage of sub-juveniles in all other areas. For this comparison we defined the central Delta to include stations 704 to 711, and 809 to 915. We focused on sub-juveniles, rather than juveniles, because according to the third hypothesis juvenile fish should be progressively moving to the lower Sacramento River and northern Suisun Bay areas. Length measurements of young delta smelt used data from the 20 mm survey to delineate sub-juveniles (see Table 1), and a one-tailed t-test was used to see if the percentage of sub-juvenile delta smelt in the central Delta was significantly greater than 50%.

Percentage data representing delta smelt distributions were $\arcsin\sqrt{x}$ transformed prior to analyses (Zar 2010). Transformed values were checked for normality with a one-sample Kolmogorov-Smirnov test. A non-parametric Wilcoxon signed-rank test was used for data addressing the second hypothesis, since the data were not transformed to normality. A test for independence of data across years showed no first- or second-order temporal correlation in any of the data series. All t-tests (or non-parametric equivalents) were run as paired tests to account for year effects.

Based on the mapped distribution of delta smelt by life-stage and the results of the statistical analyses described above, we generated two synthetic maps, consistent with publically available survey data, which can be used to represent the locations of delta smelt at two key life stages -- 1) juveniles in early summer, as they initiate a protracted period of feeding, growth, and maturation prior to dispersal to spawning areas, and 2) mature adults at or immediately prior to spawning, which reflects the maximum extent of the dispersal that they experience associated with movement to spawning areas.

Results

Distribution of delta smelt by life stage

The distributions of multiple delta smelt life stages are provided in Figures 3a through 3f. During summer months the majority of delta smelt feed, grow, and mature in four adjacent geographic locations -- in Suisun Bay and Suisun Marsh (Montezuma Slough), at the confluence of the Sacramento and San Joaquin rivers, and in the lower Sacramento River (Figure 3a). Data from the Summer Tow-net surveys show that nearly 90% of the delta smelt sampled in summer are found in that circumscribed area (Table 2). Delta smelt are essentially absent from the east and south delta during this period. While it should be noted that prior to 2011 surveys in the summertime did not extend up the Sacramento River to habitat in the Cache Slough complex of river channels in the north, nor into the Napa River and its estuary west of the Delta, data from recent surveys strongly suggest that delta smelt are likely residents in those areas in the summer (Sommer et al. 2011).

Delta smelt continue to occupy the same general locations into the autumn, with more than 80% of the sampled fish resident in the same four areas of the estuary through November, and exhibit a substantial presence in the Cache Slough area (Figure 3b). Survey data do, however, suggest some shifts in areas occupied, with increases in the percentages of total delta smelt captured in north Suisun Bay and Montezuma Slough (Table 2). Based on returns from the Spring Kodiak Trawl from January through May, it appears that a trend toward increased delta smelt numbers in areas beyond the four summer population foci continues, and expands through the winter and into the spring, with occurrences and numbers beyond the mid-year core areas in all compass directions. In the winter and spring, Delta smelt extend to the northwest into the Napa River, are more frequent north in Suisun Marsh, are found to the northeast further up into the lower Sacramento River, are frequent in the Cache Slough area, and can be found in small numbers in the eastern Delta, including the lower San Joaquin River (Figure 3c).

Approximately 80% of pre-spawning adults are sampled from just three areas -- Montezuma Slough, the lower Sacramento River, and the Cache Slough complex (Table 2). Spawning adults in the Spring Kodiak trawl are generally observed in the same locations as their pre-spawning predecessors, although there is 80% fewer spawners than pre-spawners observed in the Spring Kodiak Trawl, providing evidence that some of the fish have moved away from open-water survey sites. Data from the Beach Seine suggests adults are found beyond the boundaries of the Spring Kodiak Trawl, with observations of delta smelt well up the Sacramento River. The differences between these two surveys suggests that the mid-channel Spring Kodiak Trawl under-samples spawning adults.

Data derived from Beach Seine surveys suggest that a northerly dispersal of spawning delta smelt adults is more frequent than dispersal in east or southeast directions (Figure 3d), with just incidental observations along the San Joaquin River. The sub-juveniles produced by these spawning adults are dispersed widely throughout the delta (Figure 3e), frequently to the limit of the range of monitoring,

suggesting the reasonable possibility that more individuals exist beyond the geographic range depicted here. However, by summer (June and July), juveniles appear to have retreated to and are concentrated in areas where they will remain for the following six months: north and south Suisun Bay, the rivers confluence, and the lower Sacramento River, particularly around Decker Island, and notably, with an apparent demographic unit residing in the Cache Slough complex.

The lack of a consistent and comprehensive spatial overlap in the five fish surveys leaves several select points of delta smelt distribution and dispersal unresolved by available data. Strong inference can be used, however, to interpret from those information gaps. Regarding delta smelt occupancy of the Cache Slough area at the upper northeastern end of the range of the species -- on average 12% of the sub-adults in September and October were sampled there. Since these months precede dispersion of adults for spawning, and since Cache Slough was not routinely surveyed in the historical Summer Tow-net Survey, it might be reasonably concluded that a year-round population exists in near-freshwater circumstances in the Cache Slough area (Sommer et al. 2009, Sommer et al. 2011). The question of year-round occupancy of the Napa River is uncertain, because neither the Summer Tow-net survey nor the Fall Midwater Trawl survey samples upper reaches of the Napa River. Data from the 20mm survey indicate that spawning occurs well up the Napa River, but the lack of data from other surveys prevents a conclusion being drawn regarding a year-round delta smelt presence there.

When considering the six maps together, it is evident that a wide-ranging population, or a collection of (likely) interacting demographic units, of delta smelt can be found year-round in several areas of the Delta -- north Suisun Bay, the rivers confluence, the lower Sacramento River (around Decker Island), and in and adjacent to Cache Slough. The data used to generate those maps allow the first hypothesis -- that delta smelt move in an easterly direction from Suisun Bay at onset of spawning -- to be addressed. The percentages sub-adult delta smelt in the early fall (September and October) and pre-spawning adults that are located east of the rivers confluence are reported in Table 3. Rather than supporting the hypothesis that the relative abundance of delta smelt east of the rivers confluence increases with fish maturing to spawning condition, the percentage of the surveyed population there actually decreases; with an average of 24% fewer delta smelt being detected in surveys east of the confluence later in their life cycle (with the west-east difference significant at the 95% level).

The second hypothesis -- that delta smelt vacate Suisun Bay and the rivers confluence prior to spawning, was addressed by testing whether the percentage of pre-spawning delta smelt that reside at the rivers confluence or to the west, was not significantly different from zero. The presence of pre-spawning delta smelt at the rivers confluence and west of it averages 67%, which is significantly different from zero at the 95% level (Table 4). The hypothesis that delta smelt vacate the western portion of the estuary for purposes of spawning can be rejected.

The third hypothesis -- that subjuvenile delta smelt are found predominantly in the central Delta -- was also rejected. Data from the 20 mm trawl survey from 1995 to 2009 show that, on average, 39% of sub-juveniles were found in the central Delta, with the remaining 61% found in other locations (Table 5). Moreover, even the finding of 39% of subjuvenile delta smelt presence in the central Delta might be viewed as misleading. Stations 704, 705, 706, and 707 are located in the lower Sacramento River, from Decker Island downstream to the confluence (see locations in Figure 2). As observed on the series of Figure 3 maps, delta smelt are typically located in this area year round; therefore, much of their presence in the central Delta is not likely to be the result of seasonal dispersal. Also, this area is on the very northwest edge of the Delta, and is not usually considered part of the central delta. Removing these four stations from the central-Delta station grouping used in Table 5 reduces the average observed presence in the actual central Delta from 39% to just 12%.

Collectively, the rejection of the three hypotheses lends strong support to the perspective that spawning movement is multi-directional likely toward local freshwater inputs, rather than supporting the conceptual model describing a unidirectional eastward migration phenomenon advocated by the federal agencies.

A pair of synthetic maps depicts inter-seasonal dispersal by delta smelt (Figures 4a and 4b). Juvenile delta smelt are found in late spring 1) in the Napa River estuary, 2) from the western portion of Grizzly Bay through Suisun Bay to the Sacramento-San Joaquin rivers confluence, including Montezuma Slough and likely other larger channels in and about Suisun Marsh, 3) in areas along the lower Sacramento River extending up to and beyond the complex of small embayments and channels around Cache Slough and Liberty Island, and 4) perhaps further north upstream in the Sacramento Ship-channel. Delta smelt adults, just before and into the period of spawning, exhibit a distribution at moderate and greater densities 1) from the area around Suisun Bay and adjacent Montezuma Slough, 2) east up the lower Sacramento River into the area of Cache Slough and Liberty Island, and in lesser densities 3) in the San Joaquin River and its more northern tributaries, 4) in Montezuma Slough in Suisun Marsh, and 5) in the lower Napa River and its estuary. An east-west distributional disjunction between younger and older delta smelt in the Delta is not apparent; lesser shifts in the distribution of delta smelt within its geographic range between life stages are apparent.

Discussion

Five trawler-based fish surveys sample extensive, partially overlapping portions of the Sacramento-San Joaquin rivers delta and adjacent areas of the San Francisco estuary. The known distributional range of delta smelt has been largely informed by those surveys (Merz et al. 2012). Delta smelt range from the just east of the Carquinez Strait, through Grizzly and Suisun bays and adjacent Suisun Marsh, up-delta past the confluence of the Sacramento and San Joaquin rivers on the lower

Sacramento River, in the Cache Slough and Liberty Island complex of waterways, and in the Sacramento Ship Channel. Use of the Sacramento River north of Walnut Grove by delta smelt has been established from Beach Seine surveys. Occasional individuals can be found in eastern, southeastern, and southern portions of the Delta in the winter and spring; and very young juvenile delta smelt may be rather widely distributed across the Delta before settling into a largely northern and western Delta distributional range. Delta smelt have also been observed in a disjunct presence in lower reaches of the Napa River.

The pertinent issue addressed here is the distribution of delta smelt adults prior to spawning and their movement to locations at which spawning apparently occurs. Two alternative perspectives have been offered regarding movement by delta smelt from “rearing” areas to spawning locations. One describes a uniform, upstream migration by delta smelt from rearing areas in the west Delta to freshwater circumstances in the east. The other describes a diffuse dispersal from embayments and channels across the northern Delta, marshward to adjacent shoals and shorelines, where upland freshwater from winter and spring storms is delivered into delta waters. The two perspectives have bearing on the understanding of what constitutes habitat for delta smelt, its spatial extent, and temporal patterns of habitat occupancy, as well as determining the conservation actions that might benefit delta smelt, prioritization of those actions, and the identity of locations at which management actions might yield greatest benefits to delta smelt.

We found no evidence from data generated by seasonal surveys that delta smelt undertake unidirectional movement in late autumn and early winter toward eastern spawning areas in the Delta. Rather, spatial data are consistent with delta smelt dispersal from bay, embayment, and channel areas occupied by pre-spawner delta smelt toward freshwater inlets in nearby shores and marshes, with only a relatively small fraction of delta smelt exhibiting moving east to freshwater, including up and into the Sacramento or San Joaquin rivers. Mapped survey data indicate that most of the delta smelt in Suisun Bay head north to Montezuma Slough and Suisun Marsh to spawn. Fish in the Cache Slough complex of channels and wetlands stay in that general area. And delta smelt in the lower Sacramento River likely disperse in numerous directions -- up the Sacramento River, east toward the San Joaquin River, and west into Montezuma Slough. On average, more than 50% of pre-spawning adult delta smelt sampled are found in Montezuma Slough, more than 17% in the lower Sacramento River, and at least 12% in Cache Slough (Table 2). Given the spatial and temporal patterns of delta smelt in survey samples, it is likely that many pre-spawning delta smelt move inshore and out of the range of institutional monitoring surveys; but, survey data indicate that most adults that are ready to spawn remain in these same three general geographic areas. The data presented here contradict the depiction of delta smelt vacating the Grizzly and Suisun bay areas and the adjacent Suisun Marsh complex of wetlands to spawn in eastern portions of the Delta. In addition, survey returns appear to counter the assertion that sub-juvenile delta smelt are more frequent across the central Delta in the spring, rather than in northern portions of the estuary. Nearly two-thirds of young

juvenile fish come from survey stations from Decker Island downstream to the Sacramento-San Joaquin rivers confluence. This finding is consistent with earlier observations of the distribution of young fish; citing Radtke (1966) and Wang (1986), two decades ago Moyle et al, (1992) reported “spawning apparently occurs along the edges of the rivers and adjoining sloughs in the western delta.”

In sum, distribution maps generated from multiple, seasonal trawl surveys that regularly capture delta smelt, do not show the sort of annual, large-scale, population-wide migration event by delta smelt as has been described by the U.S. Fish and Wildlife Service and Bureau of Reclamation. The most parsimonious conclusion that can be drawn from surveys that sample delta smelt before, during, and after the winter-early spring spawning period is that the fish move from open-water circumstances to adjacent shoals and shoreline areas, which exhibit the physical attributes, especially freshwater inputs and appropriate substrates, that are necessary to support successful spawning.

Sommer et al. (2011) also recently investigated the annual dispersal patterns of delta smelt. That study invokes the centroid of the distribution of delta smelt (essentially the average position of delta smelt in temporal samples from a subset of Fall Midwater Trawl stations), suggesting that the “population” centroid moves slightly east in the very late autumn in relation to the location of the dynamic low-salinity zone in the estuary. The findings presented here clearly indicate that the centroid of the distribution of delta smelt is an inappropriate parameter for assessing the direction of the fish’s inter-seasonal movement. The west to northeast orientation of Delta channels that are occupied by delta smelt perforce can provide for an eastward component to fish spawning movements that are substantively inshore, north (or south) toward freshwater inputs. Moreover, the presence of multiple demographic foci obviates the utility of defining a single delta smelt centroid, the geographic shifting of which can only misrepresent actual site-specific movement patterns. But, perhaps most importantly, the slight eastward shifts in the centroid of the distribution of delta smelt described by Sommer et al. do not support the assertion that delta smelt migrate en mass to the freshwater edge of the Delta’s low-salinity zone – even a substantial shift in the distributional centroid of delta smelt with the onset of spawning would leave a large fraction of the fish far from the freshwater limits at the Delta’s eastern boundary.

Absent evidence of eastward, “upstream” migration by delta smelt, Sommer et al. (2011) turn to previous studies for support, asserting “...details of its upstream migration have remained elusive (Swanson et al. 1998). Delta smelt are known to inhabit the oligohaline to freshwater portion of the estuary for much of the year until late winter and early spring, when they migrate upstream to spawn. After hatching, their young subsequently migrate downstream in spring towards the brackish portion of the estuary (Dege and Brown 2004).” This description of an “upstream” migration phenomenon is consistent with the large-scale, cross-Delta movement patterns depicted on the agency maps. But neither of the studies cited provide support for the assertion made. Swanson et al. (1998) studied delta smelt

swimming performance, and while "winter migration" of delta smelt is mentioned, the authors offer no evidence of the extent of dispersal by the fish, nor would it be expected from a study of physiological phenomena. In reference to the existence of delta smelt migration, Swanson et al. cite Moyle et al. (1992). And, while Moyle et al. (1992) do refer to a "spawning migration" in their Figure 1, no data are provided in support. As for the Dege and Brown (2004) citation, it draws on sequential trawl survey returns to address seasonal shifts in the mean location of delta smelt specifically with respect to the position of the low-salinity zone in the Delta. But it does not offer data that addresses the issue of a spawning migration per se, noting "spawning occurs in freshwater with the larvae gradually moving downstream to the brackish water (1–7 parts per thousand) habitat of juveniles and adults." There is little else in the study that gives an indication of the direction or magnitude of a spawning migration. Thus, the studies cited by Sommer et al (2011), and studies cited in those studies, do not offer any documentation of eastward, upstream migration by delta smelt.

Use of the term "migration" to characterize seasonal, spawning-related movements in delta smelt certainly has contributed to a confounded dispersal narrative. The federal resource agency maps describe movement phenomena that meet the vernacular use of the term migration, with lots of fish moving extensive distances across the Delta. And, Sommer et al. (2011) used the term in asserting that a long-distance west-to-east dispersal phenomenon exists. But, Moyle (2002) and Bennett (2005) also referred to migration in describing delta smelt moving from open waters to adjacent shorelines – a not quite commonplace use of the term. Migration evokes a picture of long distance unidirectional movement to most observers, but in strict technical usage it is not the distance, rather the intent or purpose of the act of dispersing, that differentiates migration from other dispersal events (Dingle and Alistair Drake 2007, Lack 1968, Ramenofsky and Wingfield 2007). Wilcove (2006) in considering migration as a phenomenon worthy of conservation attention notes that animals "are often on the move, and not all of their wanderings fall into the category of migration." Wilcove differentiates migratory movements from "daily searches for food and shelter" or "the dispersal movements of offspring, as they establish their own territories." Notwithstanding the distances involved, he considers "seasonal back and forth journeys between two sites," including those "spread out between generations" as meeting the definition of migration. Hence, while the term migration conjures up for many a picture of songbird flights from boreal forests to far-distant tropical winter refuges, it is not technically incorrect to invoke the term migration to describe the delta smelt's far less ambitious dispersal from open waters to adjacent shorelines. That considered, we have used the term dispersal to reflect the not-coherent seasonal movement of the fish between rearing and spawning areas, and to differentiate such movements from the long-distance, unidirectional movements that are associated with certain other fish and wildlife species (including the several salmon runs with which delta smelt seasonally co-occur).

The findings presented here regarding seasonal dispersal have implications to the understanding of delta smelt ecology and behavior. Federal agency maps (in Figure 1) suggest that delta smelt exist as an open, undifferentiated population in the Sacramento-San Joaquin Delta (with a possibly disjunct demographic unit in the Napa River estuary). An annual, east-west migration of delta smelt would serve to provide contact among and mixing of individuals into a single (truly) panmictic population. But, the presence of four or more geographically discontinuous delta smelt spawning foci in the Delta, and, absent mass directional movements, a different demographic picture is indicated. Substantial demographic mixing is certain in such a scenario, but at least within each generation, exchange of individuals from areas of the western Delta (Suisun Bay and marshes) and eastern Delta (Cache Slough and neighboring areas) is likely to be limited; while allowing for the stepping-stone exchange necessary to genetically tie the demographic units of delta smelt east of the Carquinez Strait (see Fisch et al. 2011).

In light of the spatial and temporal patterns of delta smelt distribution presented here, characterization of delta smelt habitat. Extensive portions of the areas depicted on the agency maps as being seasonally occupied, hence providing habitat for delta smelt, appear to support a very small fraction of the overall numbers of the species, and then only for limited periods of the year (see Figure 4 in Merz et al. 2011). According to survey data, much of the area in the large eastern polygon on the two agency maps is infrequently occupied and currently may not provide habitat for delta smelt at all. At the same time, some areas of the west Delta, which have explicitly been considered to have limited or intermittent habitat quality (see Armor et al. 2006), appear to host delta smelt that are preparing to spawn, and those areas and adjacent channels appear to be more consistently occupied by delta smelt that previously described.

These and other distributional insights that can be gleaned from the distribution maps presented here are worthy of consideration by conservation planners and resource managers. The distribution of delta smelt during each of the life stages serves to define the suite of environmental stressors that may affect them. That a substantial portion of the estuary's delta smelt spawners are found in Suisun Marsh, but a small fraction of the youngest delta smelt are subsequently there, suggests a need for close examination of environmental stressors in that area. An ambitious effort to restore tidal marshes and wetlands in the Delta, which are believed to contribute to producing the prey that feed delta smelt, has targeted candidate locations for habitat restoration efforts (BDCP 2013). Available distribution data and the dispersal phenomena that can be inferred from them strongly suggest that marshland restoration efforts would be best directed and prioritized to areas within and between the foci of occurrences of delta smelt in the north Delta. The lack of evidence that delta smelt make an extensive easterly migration to spawn should inform the selection of locations (and prioritization) for restoration targets, with recognition that efforts to construct or rehabilitate habitats for delta smelt should be designed to support local demographic units, not seasonal migrants. Furthermore, a spatially explicit interpretation of inter-seasonal movement in delta

smelt has implications in assessing the effects of contaminants, including ammonium loading into the Delta system, on delta smelt. Data and models suggest that ammonium discharges contribute to altered nutrient ratios, with effects on the composition and abundances of phytoplankton that support the zooplankton prey base that delta smelt depend, perhaps leading to disruption of the food web and local declines in fish numbers (Glibert 2010, Glibert et al. 2011). The maps presented may indicate that certain subareas of the Delta that are unoccupied or occupied at low densities or intermittently by delta smelt may suffer from chronic poor nutrient and prey conditions, therefore, may constitute lower-quality habitat. Restoration efforts in such areas that do not address contaminant inputs to the system may be unlikely to deliver the intended benefits to delta smelt.

The maps presented here indirectly address Sommer et al.'s (2011) concern regarding the effects that entrainment of delta smelt at water export facilities in the south Delta may have on the species' status and trends, and indicate that conclusions regarding population-level effects of entrainment at export pumps may warrant reevaluation (see Grimaldo et al. 2009). While salvage samples at export pumps demonstrate that delta smelt are at least intermittently entrained, the assertion that mortality from entrainment is frequently large or is sporadically so (see Kimmerer 2008, Miller 2011, Kimmerer 2012), therefore consequential to the status and trends of delta smelt, is not so clear (and, consider Castillo et al. 2012). While relatively wide dispersal of larvae and very young juvenile delta smelt away from natal spawning areas is suggested from available distribution data, hence some proportion of the very youngest delta smelt may be lost at the pumps, the contention that large numbers of "upstream"-migrating delta smelt pass perilously close to the export facilities or are drawn to them during annual, long-distance spawn movements seems not to be supported by available survey data. .

Using available survey data, we have presented a picture of the distribution and dispersal of delta smelt prior to spawning that is complex. A diffuse collection of delta smelt population foci exist in and adjacent to the northern Delta's open waters, individuals from which undertake diffuse landward movements to spawn. The diffuse movements suggested by the seasonal distribution maps presented here are consistent with the long-understood concept that has delta smelt maturing in the estuary's brackish waters and spawning in freshwater circumstances. The maps offer no support for a unidirectional, easterly spawning migration by delta smelt from open waters in the west of the Delta to fresher waters to the east. The alternative conceptual model of delta smelt spawning movements described here, and supported by earlier studies and inferences, indicates a need to re-evaluate the relative importance of the environmental stressors that are acting to reduce the numbers of delta smelt and appropriate recovery measures that should be taken in efforts to conserve it.

ACKNOWLEDGMENTS

We gratefully acknowledge the California Department of Fish and Game, United States Fish and Wildlife Service, and the Interagency Ecological Program, especially R. Baxter, K. Hieb, R. Titus, V. Afentoulis, D. Contreras, B. Fujimara, S. Slater, J. Adib-Samii and J. Speegle for many years of data collection and its dissemination. P. Rueger and J. Melgo provided valuable data and spatial analyses. P. Weiland and L. Fryer commented extensively on earlier drafts. S. Blumenshine provided important input to the statistical analysis, and three anonymous reviewers provided insights and guidance on the penultimate draft of this manuscript. Funding for this project was provided by the Center for California Water Resources Policy and Management and the State and Federal Contractors Water Agency.

Literature cited

Alpine, A.E., J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946-955.

Armor, C., R. Baxter, W. Bennett, R. Breuer, M. Chotkowski, P. Coulston, D. Denton, B. Herbold, W. Kimmerer, K. Larsen, M. Nobriga, K. Rose, T. Sommer, and M. Stacey. 2005. Interagency Ecological Program Synthesis of 2005 Work to Evaluate the Pelagic Organism Decline (POD) in the Upper San Francisco Estuary. Interagency Ecological Program. Available online at:
http://www.science.calwater.ca.gov/pdf/workshops/POD/2005_IEPPOD_synthesis_report_111405.pdf

BDCP. 2013. <http://baydeltaconservationplan.com/Home.aspx>

Bennett, W.A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science*. Volume 3, Issue 2 (September), Article 1. Available online at:
<http://repositories.cdlib.org/jmie/sfews/vol3/iss2/art1>

Castillo, G., J. Morinaka, J. Lindberg, R. Fujimura, B. Baskerville-Bridges, J. Hobbs, G. Tigan, and L. Ellison. 2012. Pre-Screen Loss and Fish Facility Efficiency for Delta Smelt at the South Delta's State Water Project, California. *San Francisco Estuary and Watershed Science* 10(4).

Dege, M. and L.R. Brown. 2004. Effect of outflow on spring and summertime distribution and abundance of larval and juvenile fishes in the upper San Francisco estuary. *American Fisheries Society Symposium* 39: 49-65.

Dingle, H., and V. Alistair Drake. 2007. What is Migration? *BioScience* 57: 113-121.

Erkkila, L.F., J.W. Moffet, O.B. Cope, B.R. Smith, R.S. Nelson. 1950. Sacramento-San Joaquin Delta fishery resources: Effects of Tracy Pumping Plant and the Delta Cross Channel. United States Fish and Wildlife Service -- Special Scientific Report 56.

Fisch, K.M., J.M. Henderson, R.S. Burton, and B. May. 2011. Population genetics and conservation implications for the endangered delta smelt in the San Francisco Bay-Delta. *Conservation Genetics* 12:1421-1434.

Glibert, P. M. 2010. Long-term changes in nutrient loading and stoichiometry and their relationships with changes in the food web and dominant pelagic fish species in the San Francisco Estuary, California. *Reviews in Fisheries Science* 18:211-232.

Glibert, P.M., D. Fullerton, J.M. Burkholder, J.C. Cornwell, and T.M. Kana. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco estuary and comparative systems. *Reviews in Fisheries Science* 19: 358-417.

Greene, V.E., S.J. Sullivan, J.K. Thompson, W.J. Kimmerer. 2011. Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary. *Marine Ecology Progress Series* 431:183-193.

Grimaldo L.F., T. Sommer, N. Van Ark, G. Jones, E. Holland, P.B. Moyle, B. Herbold, and P. Smith. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? *North American Journal of Fisheries Management* 29:1253-1270.

Kimmerer, W.J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 6(2): Article 2. Available at <http://escholarship.org/uc/item/7v92h6fs>

Kimmerer, W.J. 2011. Modeling Delta Smelt Losses at the South Delta Export Facilities. *San Francisco Estuary and Watershed Science* 9(1). Available at <http://escholarship.org/uc/item/Ord2n5vb#page-1>

Lack, D. 1968. Bird Migration and Natural Selection. *Oikos* 19: 1-9.

Merz, J.M., S. Hamilton, P.S. Bergman, and B. Cavallo. 2011. Spatial perspective for delta smelt: a summary of contemporary survey data. *California Fish and Game* 97: 164-189.

Miller, W.J. 2011. Revisiting assumptions that underlie estimates of proportional entrainment of delta smelt by State and Federal water diversions from the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 9(1).

Moyle, P.B., B. Herbold, D.E. Stevens, and L.W. Miller. 1992. Life history of delta smelt in the Sacramento-San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 121:67-77. Available online at: [http://afsjournals.org/doi/abs/10.1577/15488659\(1992\)121%3C0067:LHASOD%3E2.3.CO%3B2](http://afsjournals.org/doi/abs/10.1577/15488659(1992)121%3C0067:LHASOD%3E2.3.CO%3B2)

Moyle, P.B. 2002. *Inland fishes of California*. University of California Press, Berkeley CA.

Nichols, F.H., J.K. Thompson, and L.E. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. *Marine Ecological Press Series* 66: 95-101.

Nobriga, M.L., and B. Herbold. 2009. The little fish in California's water supply: a literature review and life-history conceptual model for delta smelt (*Hypomesus transpacificus*) for the Delta Regional Ecosystem Restoration and Implementation Plan (DRERIP). Available online at: http://www.dfg.ca.gov/ERP/conceptual_models.asp

Radtke, L.D. 1966. Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento-San Joaquin Delta with observations on food of sturgeon. In: Turner J.L., Kelley H.B., editors. Ecological studies of the Sacramento-San Joaquin Delta. California Department of Fish and Game Bulletin 136:115-129.

Ramenofsky, M., and J.C. Wingfield. 2007. Regulation of Migration. *BioScience* 57:135-154.

Sommer, T.R., C. Armor, R.D. Baxter, R. Breuer, L.R. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W.J. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32:270-277. Available online at: <http://www.iep.ca.gov/AES/POD.pdf>

Sommer, T., F.H. Meija, M.L. Nobriga, F. Feyrer, L. and Grimaldo. 2011. The spawning migration of delta smelt in the upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* 9:2, 1-16.

Swanson, C., T. Reid, P.S. Young, and J.J. Cech. 1998. Swimming performance of delta smelt: maximum performance and behavioral kinematic limitations on swimming at submaximal velocities. *Journal of Experimental Biology* 201: 333-345.

The Bay Institute. 1998. From the Sierra to the sea: The ecological history of the San Francisco Bay-Delta watershed. Novato, CA. 286 pp.

U.S. Bureau of Reclamation. 2012. Adaptive management of fall outflow for delta smelt protection and water supply reliability. Revised milestone draft. 28 June 2012. 99 pp.

U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants; determination of threatened status for the delta smelt. *Federal Register* 58 (42): 12854-12864. Available online at: http://ecos.fws.gov/docs/federal_register/fr2235.pdf

U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants; critical habitat designation for the delta smelt. *Federal Register* 59 (242): 65256-65277. Available online at: http://ecos.fws.gov/docs/federal_register/fr2751.pdf

U.S. Fish and Wildlife Service. 1996. Recovery plan for the Sacramento-San Joaquin Delta native fishes. U.S. Department of the Interior: Fish and Wildlife Service Region 1. Available online at: http://ecos.fws.gov/docs/recovery_plan/961126.pdf

U.S. Fish and Wildlife Service. 2008. Biological opinion on the effects of the coordinated operations of the CVP and SWP in California to the threatened delta smelt (*Hypomesus transpacificus*) and its designated critical habitat. Memo 12/15/2008 to Bureau of Reclamation from Region 8 Director, U.S. Fish and Wildlife Service, Sacramento, California.

U.S. Fish and Wildlife Service. 2010. Presentation by the U.S. Fish and Wildlife Service to the National Research Council's Committee on Sustainable Water and Environmental Management in the California Bay-Delta. 25 January 2012.

van Geen, A, and S.N. Luoma. 1999. The impact of human activities in sediments of San Francisco Bay, California: an overview. *Marine Chemistry* 64:1-6.

Wang, J.C.S. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary. Technical Report 9. FS/B10-4ATR 86-9.

Wang, J.C.S. 1991. Early life stages and early life history of the delta smelt, *Hypomesus transpacificus*, in the Sacramento-San Joaquin estuary, with comparison of early life stages of the longfin smelt, *Spirinchus thaleichthys*. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary. Technical Report 28. Aug 1991. FS/BIO-IATR/91-28.

Wang, J.C.S., and Brown, R.L. 1993. Observations of early life stages of delta smelt, *Hypomesus transpacificus* in the Sacramento-San Joaquin Estuary in 1991, with a review of its ecological status in 1988 to 1990. Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary. Technical Report 35.

Wilcove, D.S. 2007. No way home: The decline of the world's great animal migrations. Island Press. Washington, D.C.

Winder, M. and A.D. Jassby. 2011. Shifts in Zooplankton community structure: Implications for food web processes in the upper San Francisco Estuary. *Estuaries and Coasts* 34:675-690.

Zar, J.H. 2010. Biostatistical Analysis. 5th Edition. Pearson Prentice-Hall, Upper Saddle River, NJ.

Table 1. *Delineation of life stages used to examine spatial dispersion of delta smelt. Monitoring program data used for each life stage description (either fish length or reproductive stage), and months and years of sampling data used in our study are*

described. Gonadal stages of male and female delta smelt found in spring Kodiak Trawl database were classified by California Department of Fish and Game (CDFG) following Mager (1986). Descriptions of reproductive stages are available at <http://www.dfg.ca.gov/delt/data/skt/eggstages.asp>

Life stage	Monitoring Program	Life Stage Distinction	Time Period	Years of data used in this study
Sub-juveniles	20-mm	≥ 15, <30mm	Apr-Aug	1995-2012
Juveniles	20-mm	30-55 mm	May-Aug	1995-2012
Juveniles	STN	30-55 mm	Jun-Aug	1987-2011
Sub-adults	FMWT	> 55 mm	Sep-Oct, Nov, Dec	1987-2012
Mature Adults: Pre-spawning	Kodiak	Reproductive stages: females 1-3, males 1-4	Jan-May	2002-2012
Mature Adults: spawning	Kodiak	Reproductive stages: females 4, males 5	Jan-May	2002-2012
Mature Adults: spawning	Beach Seine		Mar-Apr	1987-2009

Table 2. Average distribution of delta smelt observed in IEP monitoring surveys by location.

Life-stage	Sub-juvenile	Juvenile	Juvenile	Sub-adult	Sub-adult	Sub-adult	Prespaw Adult	Spawning Adult	Adult	Spawning Adult	Prespaw & Spawn
Period	All	All	Jun-Aug	Sep-Oct	Nov	Dec	Jan-May	Jan-May	Mar-Apr		
Survey	20mm	20mm	STN	FMWT	FMWT	FMWT	Kodiak	Kodiak	Beach Seine	Combined	
San Pablo Bay											
323	0.0%	0.0%	0.0%	0.1%	0.0%	0.1%					
Napa River											
340	1.3%	0.5%	0.9%	0.0%	0.0%	0.0%	2.0%	4.3%		2.7%	2.7%
342	0.5%	0.7%									
343	1.2%	0.7%									
344	1.0%	0.7%									
345	2.3%	1.3%									
346	3.4%	1.6%									
Subtotal	9.7%	5.5%	0.9%	0.0%	0.0%	0.0%	2.0%	4.3%		2.7%	2.7%
Carquinez Strait											
405	0.2%	1.9%	1.9%	1.6%	0.0%	0.1%	0.2%	0.0%		0.0%	0.0%
411	1.5%	1.8%	0.7%	0.8%	0.4%	0.3%	0.4%	0.1%		0.1%	0.1%
418	0.3%	1.1%	2.4%	2.2%	2.2%	0.5%	0.3%	0.4%		0.2%	0.2%
Subtotal	1.9%	4.9%	5.0%	4.7%	2.6%	0.9%	0.9%	0.5%		0.3%	0.3%
South Suisun Bay											
501	0.7%	2.9%	3.3%	1.5%	1.5%	6.8%	1.8%	0.3%		0.2%	0.2%
504	2.5%	1.0%	1.6%	2.0%	0.3%	0.6%	0.6%	0.2%		0.1%	0.1%
508	1.9%	3.6%	5.4%	6.9%	2.8%	2.4%	1.1%	0.6%		0.4%	0.4%
Subtotal	5.1%	7.5%	10.3%	10.4%	4.6%	9.8%	3.5%	1.2%		0.7%	0.7%
Montezuma Slough											
606	3.6%	1.5%	0.8%	2.9%	7.6%	15.7%	21.7%	14.9%		9.4%	9.4%
609	5.2%	1.7%	1.4%				26.6%	10.6%		6.7%	6.7%
610	3.8%	1.5%	1.0%	0.2%	0.2%	1.5%	2.1%	1.4%		0.9%	0.9%
Subtotal	12.5%	4.7%	3.2%	3.1%	7.8%	17.3%	50.4%	26.9%		17.0%	17.0%
North Suisun Bay (including Grizzly & Honker Bays)											
513	3.6%	6.2%	9.0%	9.1%	8.8%	4.6%	1.2%	1.9%		1.2%	1.2%
602	3.6%	16.2%	15.5%	4.1%	1.2%	4.1%	1.4%	0.5%		0.3%	0.3%
519	1.8%	7.0%	8.9%	2.9%	7.3%	16.0%	4.9%	2.5%		1.6%	1.6%
Subtotal	9.0%	29.4%	33.4%	16.1%	17.3%	24.7%	7.5%	5.0%		3.1%	3.1%
Confluence											
520	3.8%	2.3%	1.7%								0.0%
703	7.1%	7.3%		10.3%	8.4%	6.5%			1.5%	0.6%	0.6%
801	2.8%	1.7%	2.2%	1.3%	0.4%	0.2%	0.8%	0.3%		0.2%	0.2%
804	3.4%	0.9%	1.4%	0.5%	0.5%	0.1%	0.9%	0.2%	0.0%	0.1%	0.1%
Subtotal	17.1%	12.2%	5.3%	12.1%	9.3%	6.7%	1.7%	0.6%	1.5%	0.9%	0.9%
Lower Sacramento River (Decker Is)											
704	9.8%	16.5%	19.0%	15.2%	16.3%	9.7%	8.1%	8.0%		5.0%	5.0%
705	1.9%	0.5%									0.0%
706	11.4%	9.7%	15.4%	17.8%	18.6%	13.8%	6.5%	2.3%		1.5%	1.5%
707	3.8%	1.5%	5.3%	6.1%	13.3%	7.0%	2.7%	9.2%	27.2%	16.5%	16.5%
Subtotal	26.8%	28.0%	39.7%	39.1%	48.2%	30.5%	17.3%	19.5%	27.2%	23.0%	23.0%

Table 2. continued.

Life-stage	Sub-juvenile	Juvenile	Juvnile	Sub-adult	Sub-adult	Sub-adult	Prespawm Adult	Spawning Adult	Adult	Spawning Adult
Period	All	All	Jun-Aug	Sep-Oct	Nov	Dec	Jan-May	Jan-May	Mar-Apr	
Survey	20mm	20mm	STN	FMWT	FMWT	FMWT	Kodiak	Kodiak	Beach Seine	Combined
Cache Slough Complex										
711	0.1%	0.0%	0.0%	5.2%	1.4%	3.4%	0.2%	3.5%	10.6%	6.3%
712							0.0%	0.5%		0.3%
713							1.0%	4.5%		2.9%
715							4.0%	9.5%		6.0%
716	5.5%	6.5%		7.3%	5.2%	2.7%	7.2%	18.1%	5.7%	13.7%
719										
798										
Subtotal	5.6%	6.5%	0.0%	12.4%	6.6%	6.1%	12.3%	36.1%	16.3%	29.2%
Upper Sacramento										
717									5.5%	2.2%
724									2.2%	0.9%
735									4.8%	1.9%
736									11.6%	4.5%
749									19.0%	7.5%
Subtotal							0.0%	0.0%	43.1%	16.9%
Lower San Joaquin River										
802				1.6%	2.0%	1.4%				0.0%
809	5.4%	0.7%	1.8%	0.2%	1.0%	1.8%	2.8%	2.9%	0.0%	1.8%
812	1.8%	0.1%	0.1%	0.1%	0.6%	0.4%	0.6%	1.5%		1.0%
815	1.9%	0.0%	0.2%	0.0%	0.0%	0.0%	0.3%	1.0%		0.6%
Subtotal	9.1%	0.8%	2.1%	1.9%	3.6%	3.7%	3.7%	5.5%	0.0%	3.4%
South Delta										
901	0.8%	0.1%								
902	0.7%	0.1%		0.0%	0.0%	0.0%	0.2%	0.3%	0.0%	0.2%
914	0.3%	0.0%		0.0%	0.0%	0.0%			0.0%	0.0%
915	0.2%	0.0%		0.0%	0.0%	0.0%			0.0%	0.0%
918	0.2%	0.0%		0.0%	0.0%	0.0%			0.0%	0.0%
Subtotal	2.2%	0.1%	0.0%	0.0%	0.0%	0.0%	0.2%	0.3%	0.0%	0.2%
East Delta										
906	0.5%	0.0%		0.0%	0.0%	0.0%			0.1%	0.0%
910	0.1%	0.1%		0.0%	0.0%	0.0%			0.1%	0.0%
912	0.0%	0.1%		0.0%	0.0%	0.0%			0.0%	0.0%
919	0.2%	0.1%		0.0%	0.0%	0.0%			0.2%	0.1%
920										
921										
922									2.5%	1.0%
923									4.2%	1.6%
Subtotal	0.9%	0.2%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	7.0%	2.8%
Total	100%	100%	100%	100%	100%	100%	99%	100%	95%	100%

Table 3. *Percentage of delta smelt sub-adults located east of the confluence in September and October in the FMWT compared with the percentage of pre-spawning adults in the subsequent Spring Kodiak Trawl.*

Cohort Year	Percentage east of confluence during Sep-Oct in FMWT	Percentage East of confluence during subsequent Jan-May in Kodiak Trawl	Change
2001	90.9%	18.1%	-72.8%
2002	52.7%	61.4%	8.7%
2003	83.3%	17.2%	-66.1%
2004	93.3%	28.2%	-65.1%
2005	76.0%	18.4%	-57.6%
2006	40.9%	26.2%	-14.7%
2007	23.8%	75.3%	15.5%
2008	73.3%	57.6%	-15.7%
2009	62.5%	2.0%	-60.5%
2010	34.1%	27.6%	-6.5%
2011	4.7%	35.8%	31.1%
Average	57.8%	33.4%	-24.4%
Std Dev.	29.1%	22.2%	43.1%

Table 4 -- *Percentage of delta smelt pre-spawning adults located at the confluence and west of it in the Spring Kodiak Trawl.*

Year	Pre-spawning Adults Jan-May
2002	81.9%
2003	38.6%
2004	82.8%
2005	71.8%
2006	81.6%
2007	73.8%
2008	24.7%
2009	42.4%
2010	98.0%
2011	72.4%
2012	64.2%
Average	66.6%
Std Dev	22.2%

Table 5. *Percentage of delta smelt sub-juveniles located in the central Delta, using data from the 20mm survey and life stage delineations from Table 1.*

<i>Year</i>	<i>Central Delta 704-711, 809-915</i>
<i>1995</i>	<i>2.3%</i>
<i>1996</i>	<i>8.8%</i>
<i>1997</i>	<i>69.4%</i>
<i>1998</i>	<i>1.2%</i>
<i>1999</i>	<i>29.1%</i>
<i>2000</i>	<i>33.8%</i>
<i>2001</i>	<i>85.4%</i>
<i>2002</i>	<i>70.3%</i>
<i>2003</i>	<i>34.7%</i>
<i>2004</i>	<i>69.4%</i>
<i>2005</i>	<i>6.9%</i>
<i>2006</i>	<i>1.4%</i>
<i>2007</i>	<i>77.2%</i>
<i>2008</i>	<i>80.0%</i>
<i>2009</i>	<i>59.7%</i>
<i>2010</i>	<i>33.5%</i>
<i>2011</i>	<i>1.0%</i>
<i>2012</i>	<i>31.9%</i>
<i>Average</i>	<i>38.7%</i>

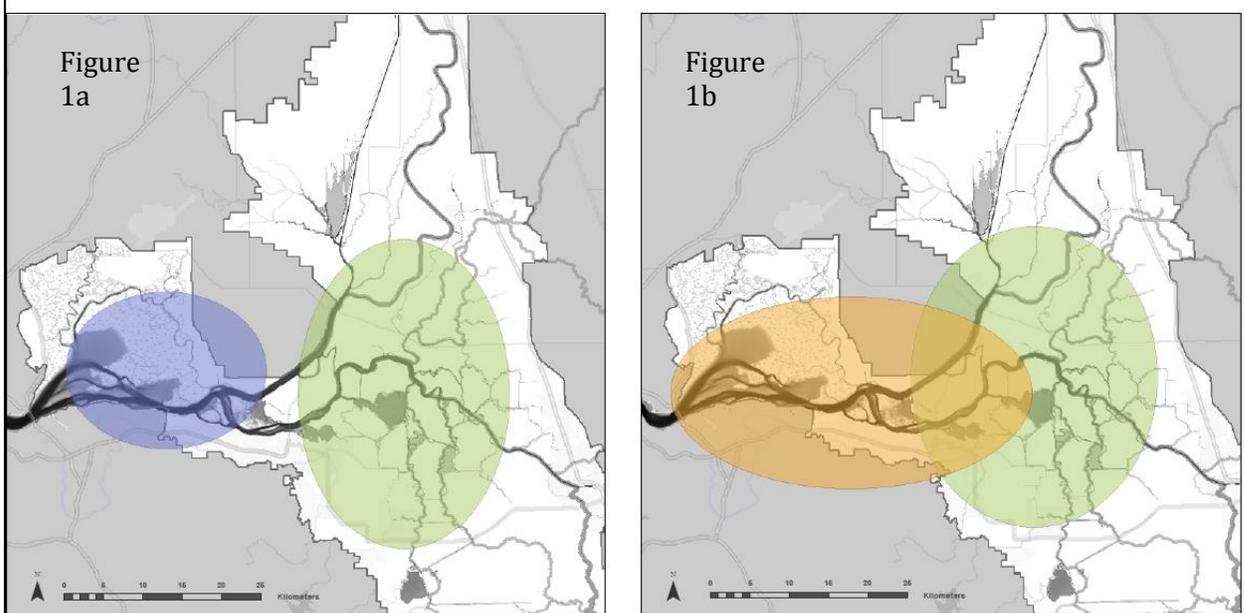


Figure 1. *Conceptual mapped distributions of and inferred seasonal dispersal by delta smelt in the San Francisco estuary redrawn from a presentation by the U.S. Fish and Wildlife Service (2010) -- left panel -- and a guidance document from U.S. Bureau of Reclamation (2012) -- right panel. The figure (a) portrays a migration of adult delta smelt from the Suisun Bay and the area of the Sacramento-San Joaquin rivers confluence (blue oval) to the central Sacramento-San Joaquin Delta in the winter and spring (green oval) prior to spawning. . Offspring migrate back from the central Delta, returning to the western distributional footprint by summer. The figure (b) depicts a shift of individuals eastward from a larger pre-spawning distribution from edge of Suisun Bay in the west to up into the lower Sacramento and San Joaquin rivers to the east (orange oval) to the central delta (green oval) where spawning presumptively occurs.*

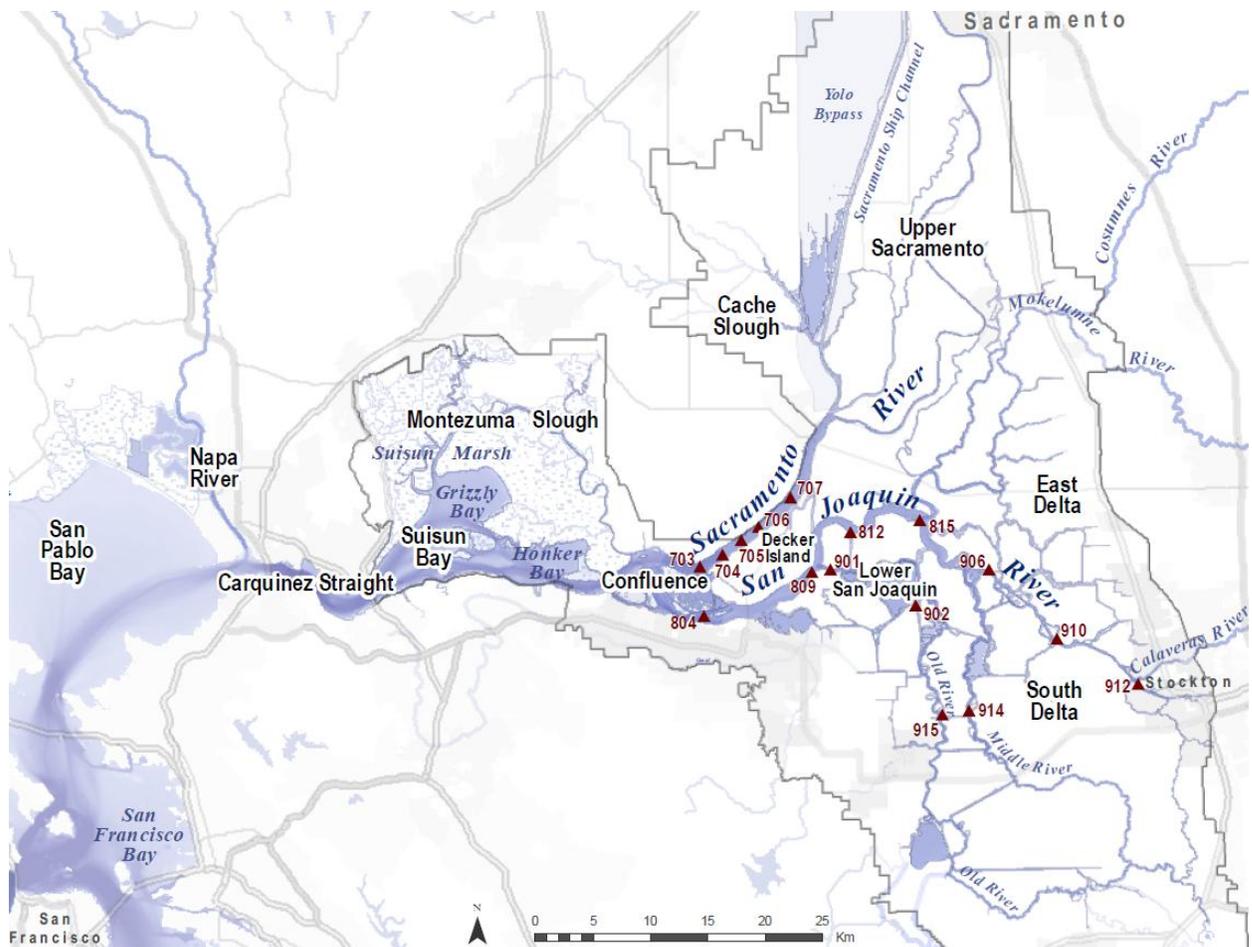


Figure 2. *The San Francisco estuary, including features and geographic designations referenced and described throughout this presentation. Numerical designations accompanying triangles identify trawl survey locations referenced in the text.*

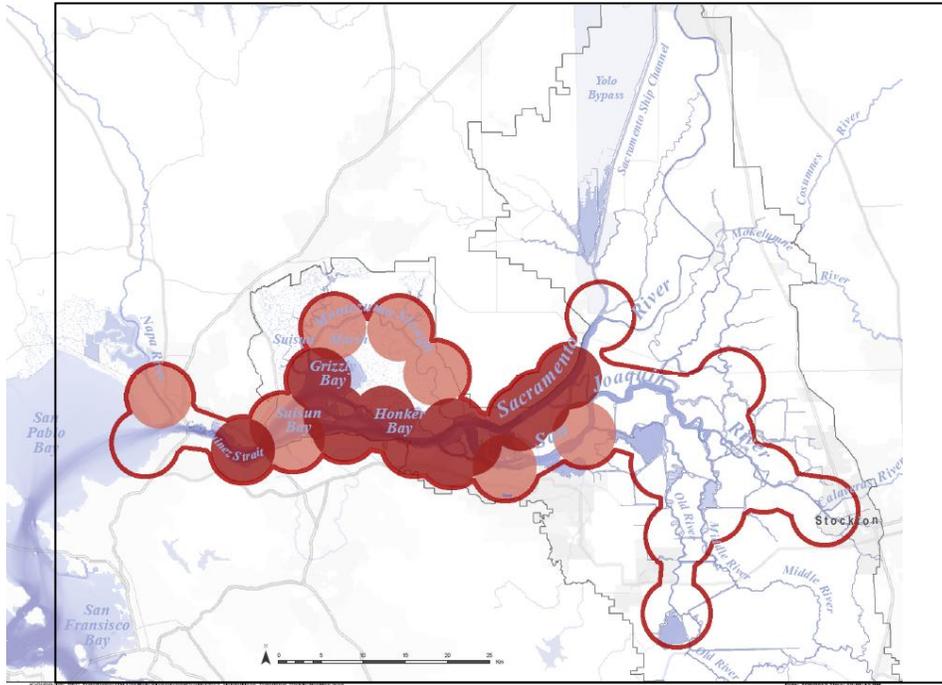


Figure 3a. Distribution of delta smelt juveniles in summer (July) in the Summer Tow-net Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.

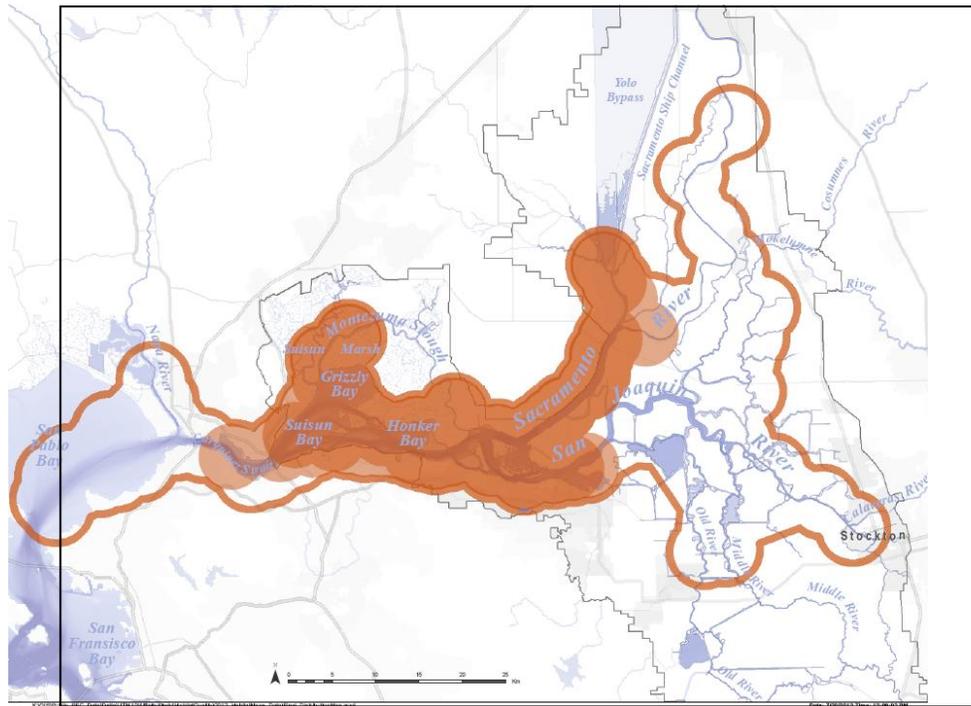


Figure 3b. Distribution of delta smelt sub-adults in fall (September to November) in the Fall Midwater Trawl. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.

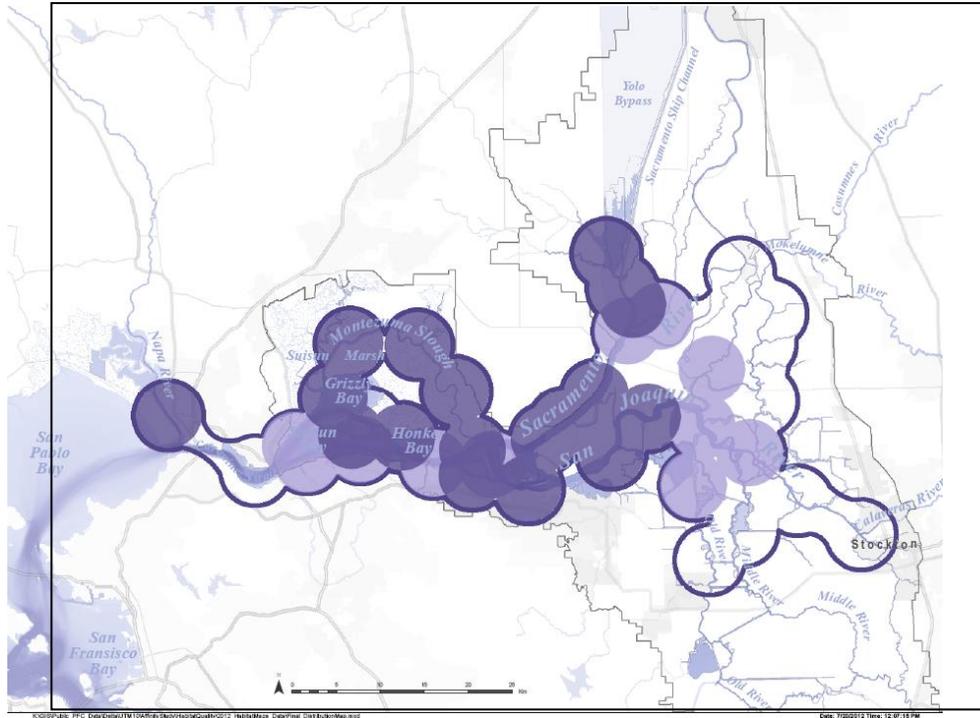


Figure 3c. *Distribution of delta smelt adults in winter (Jan to May) in the Spring Kodiak Trawl. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.*

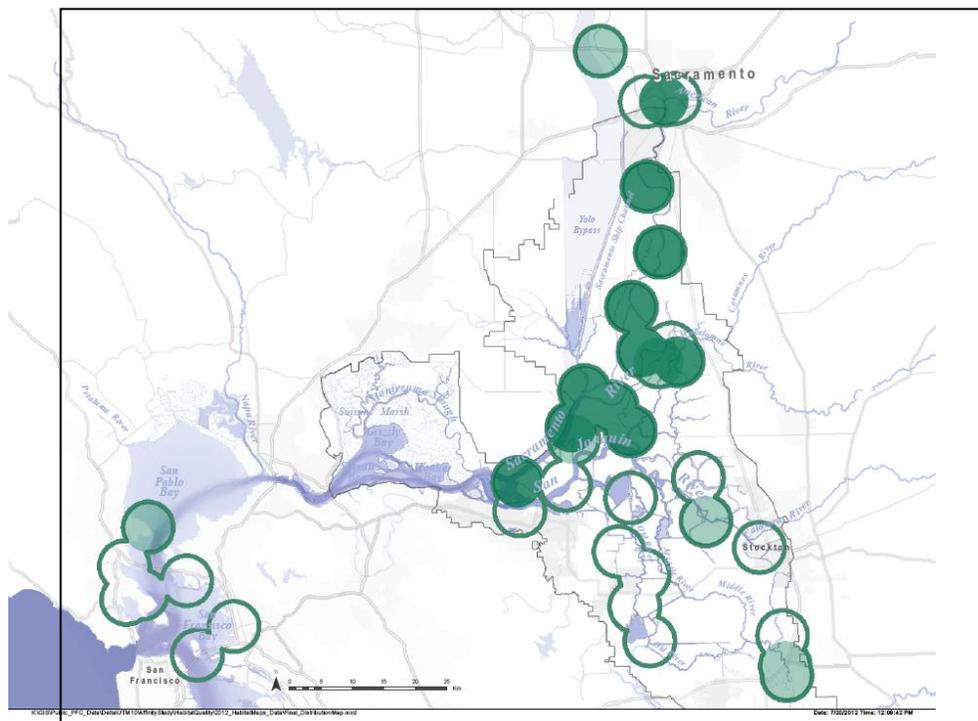


Figure 3d. Distribution of delta smelt adults in spring (March to April) from the Beach Seine Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.

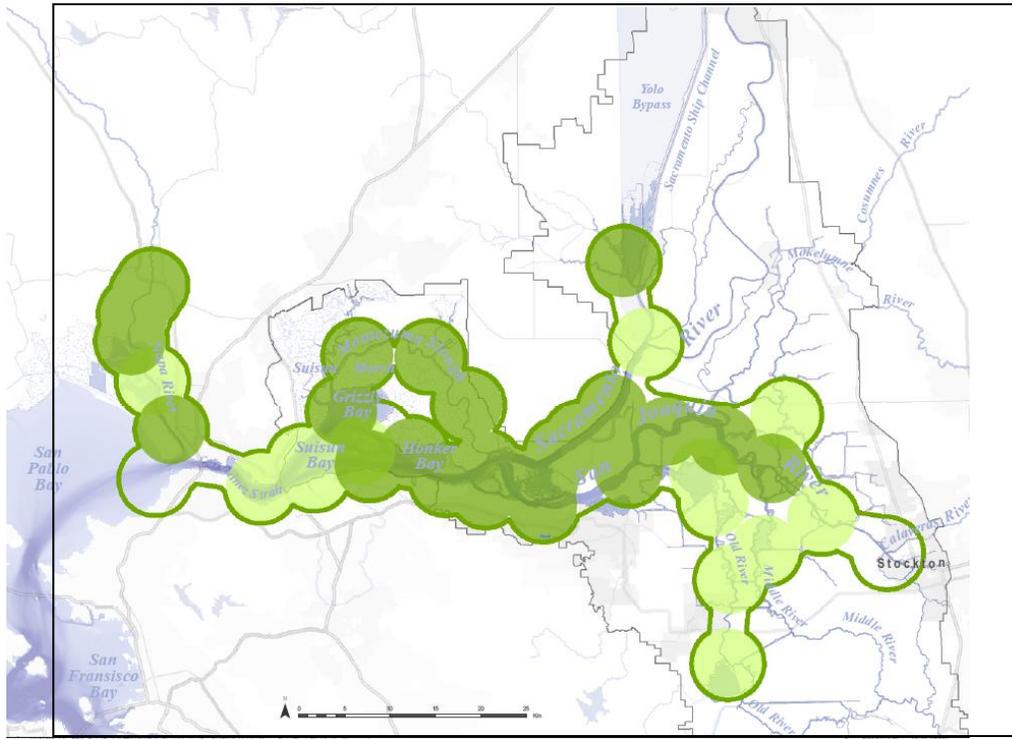


Figure 3e. Distribution of delta smelt sub-juveniles in spring (April to June) in fall the 20 mm Survey. Dark circles show survey stations collectively comprising 90% of observed catch. Light circles show next 9% of observed catch. Solid line indicates extent of survey for consistently surveyed stations. A 4km buffer was utilized for all stations.

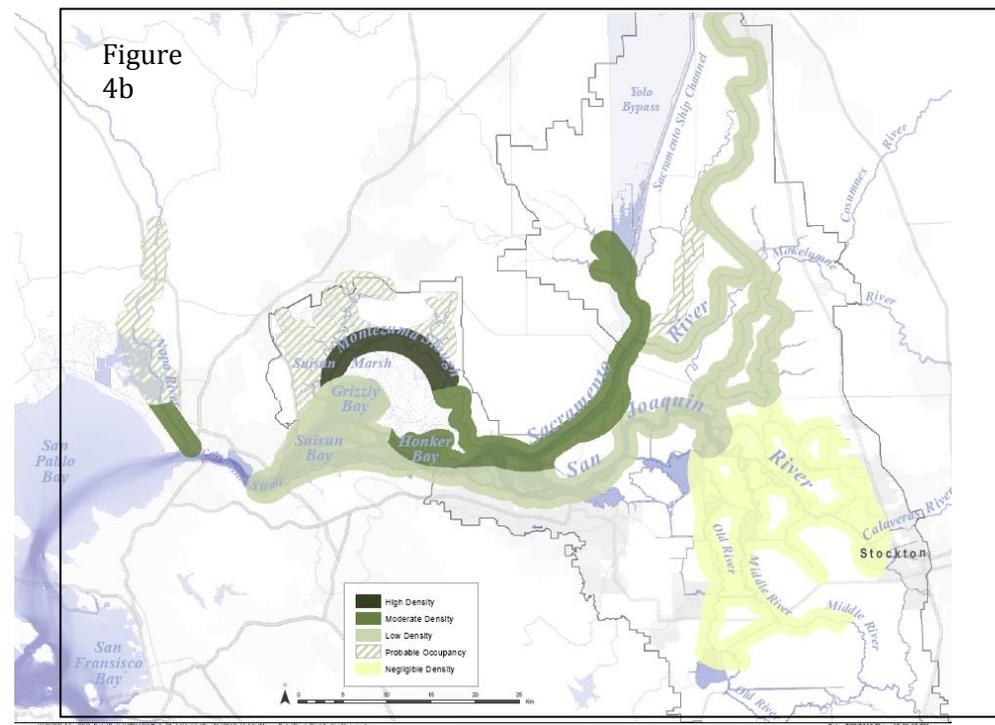
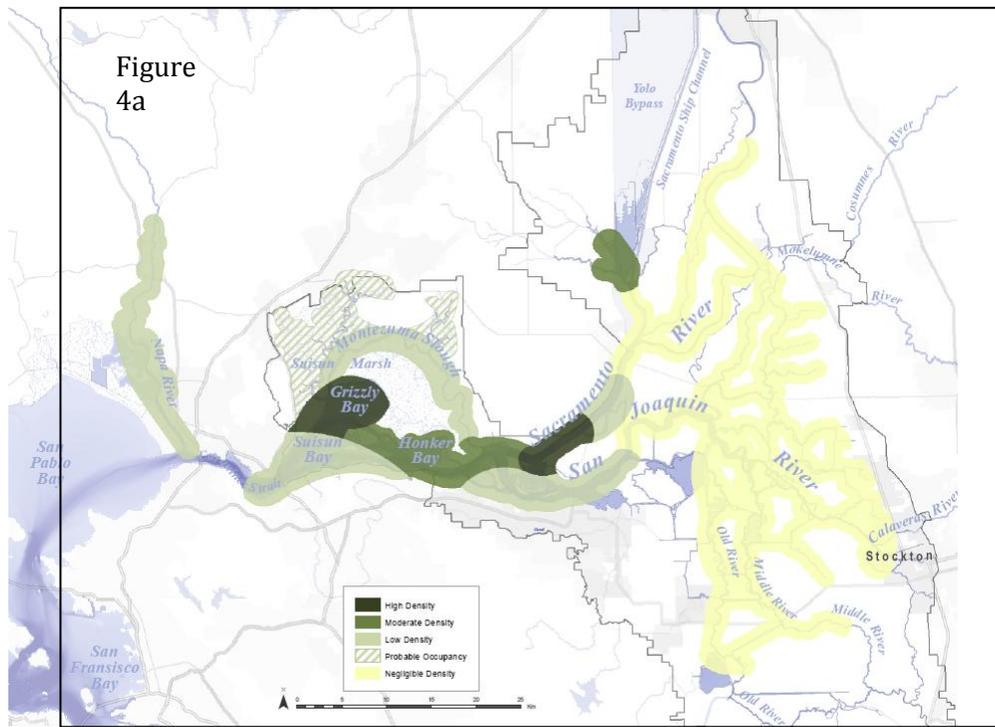


Figure 4. Synthesized distribution of delta smelt in summer/fall (top panel) before dispersion to spawning areas, and in spring (bottom panel) after dispersion. The dark areas show the predominant range during each period. The high and moderate density areas combined account for 90%, on average, of the observed presence of delta smelt.

Habitat affinity analysis as a tool to guide environmental restoration for an imperiled estuarine fish: the case of the delta smelt in the Sacramento-San Joaquin Delta

Dennis D. Murphy
Biology Department
University of Nevada
Reno, Nevada 89557

Scott A. Hamilton
Center For California Water Policy and Management
1017 L Street, Suite 474
Sacramento, CA 95814

ABSTRACT

Habitat restoration efforts in the Sacramento-San Joaquin Delta in central California move forward under the state's ambitious Bay Delta Conservation Planning process, despite a paucity of information on the habitat needs of many of the plan's targeted species. The endemic delta smelt, protected as threatened under the federal Endangered Species Act, is a primary focus of those efforts despite key uncertainties regarding many aspects of its relationship with the estuary's physical and biotic resources. Here we carry out habitat affinity analysis for multiple life stages of the delta smelt drawn from time-series data from four trawl surveys, and data on environmental attributes taken from throughout the distribution of the fish. Ranges of conditions acceptable to delta smelt for each of seven environmental attributes were identified. Low turbidity and high water temperatures render a large portion of the estuary seasonally unacceptable to delta smelt. Within areas that experience largely acceptable water quality conditions, patterns of delta smelt occurrences indicate that habitat occurs where deep channels adjoin shallow-water circumstances and extensive patches of emergent vegetation. Habitat suitability indices show that favored environmental circumstances vary with life stages, and delta smelt move as they mature to access suitable areas with environmental attributes in acceptable ranges. Areas that exhibit highest geometrically weighted average HSI values for environmental attributes are displayed on maps, and can be viewed as representing potential priority target areas for habitat restoration efforts. Delta smelt should benefit in priority target areas with channel modification and directed wetlands restoration efforts.

Keywords – delta smelt, habitat, habitat affinity analysis, habitat suitability index.

Introduction

The need for reliable knowledge regarding the habitats of imperiled species frequently outstrips available information (Karieva et al. 1998, Johnson et al. 1999, Reed et al. 2006). A paucity of data and observations can stymie planning even for the flagship species and their habitats that are the focal targets in those conservation efforts. Planning for species with particularly narrow distributions, very limited numbers, and especially cryptic behaviors can be challenged by a lack of observations, and constrained by limited data sets from which species-habitat relationships can be gleaned. Examples abound, from conservation efforts for the few remaining marbled murrelets, sea birds nesting high in old growth and late seral forests along the northern Pacific Coast (Peery 2004, USFWS 1997), to attempts to provide beneficial hydrodynamics for the pallid sturgeon, a species sparsely distributed in the murky depths of the lower Missouri River (Bajer and Wildhaber 2007, USFWS 2013). One federally protected species suffering from an incomplete understanding of its habitat requirements is the narrowly endemic delta smelt from central California's Sacramento-San Joaquin Delta and adjacent areas of the San Francisco estuary. The elusive delta smelt's ecological relationships are obscured under turbid waters, and many of the essential attributes of its habitat are still the subject of surmise, rather than hard data (see Sommer and Meija 2013). Two decades after its listing as a threatened species, it actually has yet to be observed to reproduce in nature (Bennett 2005).

The limited understanding of essential habitat attributes of the diminutive delta smelt has contributed to strident disagreement regarding necessary management actions to protect

the species that culminated in litigation pitting the federal and state governments against one another (Consolidated Delta Smelt Cases, 717 F. Supp. 2d 1021 [E.D. Cal. 2010]). The need for an understanding of the ecology of the delta smelt and the resources that support it is immediate, reflecting its role as a focal species in the Bay-Delta Conservation Plan, an ambitious effort to restore and manage the most extensive and environmentally disrupted estuary on the Pacific Coast (BDCP 2013). Plan architects hope to restore and enhance delta smelt habitat in order to bolster the fish's numbers and enhance the likelihood of its persistence, noting that its actual numbers can only be speculated upon (see Bennett 2005, Kimmerer 2008, Newman 2008, Kimmerer et al. 2009), its patterns of dispersal are the subject of ongoing debate (Sommer et al. 2011, Murphy and Hamilton 2013), and the causes of its imperilment appear to be many, but are largely not quantified (see Feyrer et al. 2007, Nobriga et al. 2008, Grimaldo et al. 2009, Winder and Jassby 2010). The current draft Plan calls for the restoration of delta smelt habitat and that of co-occurring species, with commitments of funding of hundreds of millions of dollars over decades. Yet what actions those habitat restoration efforts should entail, where they should be carried out, and how they might be prioritized remains in fair doubt (NRC 2011). It is the purpose of this study to draw inference from publically available survey data on delta smelt and concurrently gathered data on environmental attributes regarding the ecological conditions that contribute to habitat for the fish, and identify areas of the Delta and adjacent estuary that are inappropriate targets for restoration efforts, thereby guiding those conservation activities to locations that offer greater promise for BDCP program success.

A holistic description of delta smelt habitat that can be used to guide actions to manage and recover the fish, direct programmatic monitoring efforts to better assess its numbers and distribution, and provide a basis for evaluating the success of conservation activities and expenditures remains elusive. But, at least some of the basic ecological needs of delta smelt have been inferred from a number of retrospective studies using a combination of time-series survey data taken in trawls that are designed to sample pelagic fishes in the estuary, paired with long-term environmental data on a number of water quality parameters, landscape attributes, and biotic factors near sampling stations (see Bennett 2005 for a then-contemporary summary, and Sommer and Meija 2013)). Much of that same information has been used to inform a number of conceptual models that provide descriptions of pathways by which environmental variables are believed to directly and indirectly contribute to determining delta smelt numbers and distribution (Armor et al. 200x, Baxter et al. 200x, Nobriga and Herbold 2009, Miller et al. 2012). Dozens of ongoing studies are extending efforts to address discordant patterns of variation in the constellation of environmental attributes of the Delta that seem likely to affect the distribution and abundance of delta smelt, but critical uncertainties undoubtedly will freight conservation planning for some time to come.

What is generally agreed upon is that the delta smelt's geographic range is narrow and diminished from its historical extent (Whipple et al. 2012). Delta smelt reside in a more or less continuous distribution, from freshwater circumstances in the north Delta, west across the confluence of the Sacramento and San Joaquin rivers in tidally influenced waters, to the western portions of Suisun Bay and Suisun Marsh. A satellite population is sometimes

found further west in the lower Napa River and its estuary. The species' distributional range in the San Francisco estuary is a scant 50 kilometers (see Merz et al. 2012), across which the delta smelt is found in open waters during most of its annual life cycle, and from which the fish appears to disperse seasonally to shoreline situations, where it spawns in and adjacent to freshwater inlets to the estuaries more saline waters (Moyle et al. 1992, Bennett 2005, Murphy and Hamilton 2013).

Several recent multivariate studies offer a lens into inter-year responses of delta smelt to a number of environmental attributes of the Delta, therefore provide some fundamental guidance to conservation planners. Feyrer et al. (2007) considered the roles of salinity, turbidity, and temperature in determining the distribution of delta smelt in a portion of its low-salinity-zone range in the San Francisco estuary, finding that the former two water-quality variables explained about a quarter of variance in the distribution of the fish. Thomson et al. (2010) used change-point analysis to investigate step changes in nearly two-dozen environmental factors, many that contribute to the extent and quality of delta smelt habitat. The authors found that reductions in turbidity and the increases in the volume of water exports in winter months corresponded with declines in delta smelt numbers that have been recorded over the past decade. MacNally et al. (2010) used multivariate autoregressive modeling to evaluate 54 fish-environmental factor relationships, including the factors considered by Thomson et al., and found generally weak relationships, but enhanced signals from food availability and the position of the low-salinity zone in the spring correlated with delta smelt numbers. Maunder and Deriso (2011) used a multistage life-cycle model that varied levels of presumptive density

dependence to consider environmental factors acting on delta smelt abundance. The study found a substantive deterministic relationship to be the availability of the fish's food resources, and signals of effects of predator abundance and temperature on different delta smelt life stages. The environmental data in that study were shared in a multivariate regression analysis by Miller et al. (2012), who asserted that their specification of environmental variables was spatially and temporally rectified to better reflect within-Delta patterns of environmental variation. Among habitat attributes, they found food availability to be a major explanatory variable in dictating population responses in delta smelt, with overarching effects from density dependence. The findings from these studies, considered in the context of inferences that can be drawn from the several available conceptual models contribute to identifying a number of essential attributes of delta smelt habitat, and the physical and biotic resource conditions that contribute to determining habitat extent and quality.

To assess the importance of habitat attributes to delta smelt and, at the same time, to offer at least contingent guidance to agency managers charged with constructing, restoring, and rehabilitating delta smelt habitat, we followed the approach of Guay et al (2000), applying habitat affinity analysis in conservation planning. Guay et al. considered the relevance of water depth, substrate composition, and water velocity to the quality of habitat for juvenile Atlantic salmon in a reach of the Sainte-Marguerite River. They divided the water body into "tiles" (geographic segments of the river), which were smaller than, but analogous to sampling stations in the San Francisco estuary, and collected attribute and fish data for areas where fish were observed and not observed. They developed preference curves for

discrete interval ranges of each attribute by comparing the percentage utilization of an interval with the percent availability of it. Preference indices ranged from 0 (considered poor habitat) to 1 (considered best habitat). Utilizing a multiplicative regression analysis, they developed a weighted habitat suitability index (HSI) enabling them to rank the quality of the habitat at any site based on the attributes at that location. Applying the techniques developed by Guay et al, we develop habitat suitability indices in an effort to parameterize descriptions of the direct and indirect effects and influences of physical and biotic attributes of the estuary on delta smelt. We draw from publically available trawler-based survey data on the distributions and relative abundances of multiple life stages of the delta smelt, and relate those demographic data to data available on physical and biotic attributes of the estuary, including bathymetric data derived from USGS databases, to inferentially identify landscape characteristics that may contribute to delta smelt habitat. We endeavor to inform habitat restoration for delta smelt by following a sequence of steps.

First, drawing on agency-generated conceptual models that articulate hypothesized, inferred, and established relationships between delta smelt and environmental variables, we identify candidate environmental attributes that appear to contribute to the extent and quality of habitat for delta smelt. Second, we use affinity analyses, in which we compare the frequency of delta smelt co-occurrence with the availability of physical and biotic resources and their spatially and temporally varying conditions to infer how environmental attributes determine the distribution of delta smelt at each of its life stages. Third, we utilize the results of the affinity analysis to develop suitability indices for each deterministic attribute separately, and then combine the suitability indices to derive

numerical meta-indices of aggregated habitat quality for each life stage using multiple regression analysis. The approach permitted us to identify specific environmental attributes that are relevant to delta smelt when several are considered simultaneously in a comprehensive treatment of its habitat. Having identified important habitat attributes, we are able to determine the environmental factors that are lacking or appear to fall out of the range of acceptable conditions for delta smelt, and where those circumstances occur in support of efforts to inform the selection of locations and prioritization of potential restoration projects.

Carrying out these steps we find it possible to offer substantive guidance to agency managers and technical staff. The results of our analysis offer prescriptions on (at least) two spatial scales. First, delta smelt distribution data mapped on three physical variables indicate that broad geographic portions of the contemporary estuary may not be appropriate targets for mechanical habitat restoration efforts because one or more physical variables, which are not under management control, fall outside ranges acceptable to the fish. Efforts to restore habitat structure and function in those locations appear to be unlikely to result in the local (re)establishment of delta smelt occupancy, or increased delta smelt numbers. Second, in situations not so constrained, the mapped habitat-affinity relationships that we have generated can be used to identify locations that appear to be suitable targets for restoration and assist in identifying the habitat-enhancing actions that might contribute to supporting delta smelt. This application of habitat affinity analysis to provide limited guidance to restoration efforts in the Delta seems apt. In effect, we infer from patterns of presence and absence of delta smelt in the estuary conditions that are

favorable for the species and thereby identify locations that may be suitable sites for restoration, because they approximate some of the conditions that are associated with the presence of delta smelt. Arguably more importantly, planners can use the affinity analysis and habitat suitability indices to avoid areas wherein restoration efforts are likely to be unsuccessful.

METHODS

Study system

The San Francisco Estuary is the largest of its kind along the U.S. Pacific Coast (Rosenfield and Baxter 2007). Formed by the confluence of the Sacramento and San Joaquin rivers watersheds, the estuary drains nearly 40% of California's surface area (van Geen and Luoma 1999, Sommer et al. 2007). The estuary is tidally influenced, with fresh river water from the east mixing with saline ocean water from the west. The major water bodies within the estuary include the Sacramento-San Joaquin Delta (Delta), which lies east of the confluence of the Sacramento and San Joaquin rivers, Suisun Bay, Carquinez Strait, and the Napa River, as well as San Pablo and San Francisco bays to the west (Figure 1). The internal estuary is highly altered from its pre-settlement physiognomy, existing now as a network of mostly fortified waterways surrounding a patchwork of subsided islands behind earthen levees. The extensive marshlands that previously dominated the estuary and the floodplains that surrounded it have largely been replaced by cultivated agriculture.

Two native fishes – the Sacramento perch (*Archopilites interruptus*) and thicktail chub (*Gila crassicauda*) – vanished with the post-Gold Rush settlement, conversion, and utilization of the estuary, as extensive tule-dominated wetlands that were dissected by dendritic channels and subject to complex tidal currents were diked and dredged. The estuary now supports a limited assemblage of native fishes; some are resident, some are anadromous transients, and several are endemic, notably the federally protected delta smelt. But the delta smelt and the rest of the native fishes now exist in communities dominated by non-native competitors and predators, supported by a highly altered food web and local shortages of essential habitat-defining environmental features and resources. Against that background, resource managers in the San Francisco estuary are challenged to identify conservation actions that will contribute to sustaining an imperiled native fishery and contribute to the recovery of listed species from inferences of those species ecological relationships and habitat needs.

Candidate habitat attributes

We began by developing a list of candidate environmental attributes that previously had been observed or surmised to potentially contribute to habitat quality for estuarine fish. These include turbidity, salinity, temperature, dissolved oxygen, pH, aquatic vegetation, prey density, water depth, substrate composition, and the extent of adjoining marshlands (see Pardue 1983, Weinstein 1986, Stier and Crance 1985, Brown et al. 2000 for lists). Environmental factors that are suspected to affect delta smelt are only slightly more limited in number (Armor et al. 2005, Baxter et al. 2005, Bennett 2005, and Nobriga and

Herbold 2009 for conceptual models and natural history syntheses). Federal and state agency scientists have hypothesized that three standard water quality factors, salinity, turbidity, and temperature, affect habitat quality (Feyrer et al. 2007, Nobriga et al. 2008). Water temperature has an influence on spawning (Wang 1986, Meng and Matern 2001, Bennett 2005, Feyrer 2004, Grimaldo et al. 2004, Sommer et al. 2004), embryo survival (Moyle 2002, Mager et al. 2004), available habitat during the summer (Nobriga et al. 2008), and adult survival (Swanson et al. 2000). Hieb and Fleming (1999) suggest that delta smelt are found across a near estuary-wide range of salinity conditions. It has been asserted that delta smelt prefer turbid water, perhaps for successful feeding (Baskerville-Bridges et al. 2004, Mager et al. 2004), and because it may reduce susceptibility to predation.

Investigators have described the calanoid copepod prey that support delta smelt (Lott 1998, Nobriga 1998 and 2002). Two multivariate analyses of an array of environment attributes of the Delta identified prey abundance as the primary determinant of population dynamics in delta smelt (Maunder and Deriso 2011, Miller et al. 2012). The fish is often described as frequenting shoals adjacent to deeper channels (Moyle 2002), with an assumption that emergent wetlands contribute to productivity at the base of the food web that supports the delta smelt. Hobbs et al. (2006) linked superior nursery conditions to increased feeding success; and other studies have recognized the potential importance of fish access to wetlands and floodplains (see Lindberg and Marzula 1993, McIvor et al. 1999). Moyle et al. (1992) and Bennett (2005) indicate that spawning occurs near estuary and river shorelines and adjoining sloughs. Substrate composition may be important in determining spawning habitat (Moyle 2002). McGowan (1998, and McGowan and Marchi

1998) found that areas inhabited by the invasive water-weed *Egeria densa* are not typically inhabited by native fish in the estuary, including delta smelt, and that low abundance of delta smelt is generally associated with areas supporting higher concentrations of submerged aquatic vegetation of all types (see also Nobriga et al. 2005, Grimaldo et al. 2009). Lehman et al. (2010a) document low delta smelt abundances in areas subject to episodic blooms by the toxic blue-green alga *Microcystis*.

From the preceding sources and agency-generated conceptual models we organized a list of candidate environmental attributes for consideration in habitat affinity analyses for delta smelt (Table 1).

Data Sources and Treatment

Fish surveys -- A synthetic description of delta smelt habitat must consider suites of environmental attributes and thresholds that act on its individual life stages. Habitat extent and quality, and the geographic location of habitat may vary between life stages; concomitantly, different sites within the estuary may be suitable or unsuitable for the fish at different stages in its life cycle. The California Department of Fish and Wildlife carries out multiple surveys of Delta fishes, returns from which include delta smelt in temporal samples that span its annual life cycle. Surveys include the 20 mm Survey, Summer Trawl Survey (STN), Fall Midwater Trawl (FMWT), and Spring Kodiak Survey, which sample extensive areas of the Delta and collect delta smelt in meaningful numbers. The methods for these surveys have been documented previously (Moyle et al. 1992, USFWS 2004,

Bennett 2005); the varying strengths and weaknesses of several of these surveys as population assessment tools for delta smelt have been discussed in detail by Bennett (2005). We used data from these publicly available fish surveys, delineating life stages as depicted in Table 2, to assess the distribution in local densities of delta smelt. We utilized data from consistently surveyed stations; that is, stations that were surveyed in every year, or in every year but one since 1995, to ensure multiple observations at sites. The time period represented for each life stage reflects the months when that life stage typically predominates among sampled delta smelt. On average, more than 75% of individuals from a given life stage were sampled during the temporal windows presented. Because year-to-year variation exists in the timing of the appearance of each life stage, we considered the period during which 90% of the specific life-stage was sampled. Doing so, we excluded the temporal extremes when habitat attributes and delta smelt presence are less certain due to the very small numbers of individuals sampled. For the FMWT, however, we considered only the months of September and October, rather than the full period of the survey through December; the first two months of the trawl period had been identified by CDFW as the basis for regulatory decisions.

Covariate Specification -- In order to assess the relative influence of local and regional environmental factors that operate to determine delta smelt occurrences, we considered habitat associations at two spatial scales -- site and regional. At the site scale we addressed covariates using data drawn from individual monitoring stations – either as data collected that were taken along with fish samples (temperature, salinity, and turbidity), or as geographic and bathymetric data drawn from geographic areas adjacent to those stations

(depth, area of shallows, channel width, distance to wetlands). Additionally, we collected data on substrate composition in March 2010 at stations where water depth was less than seven meters, classifying substrates using delineations in Table 3. At the regional scale we considered factors that operate at broader spatial scales (including water body type, prey availability, and predation pressure). Specification of these attributes is provided in Table 3.

Not unexpectedly, upon investigating data availability, we found insufficient data to support the inclusion of some variables in the affinity analyses. Specifically we were unable to obtain suitable data on dissolved oxygen, pH, contaminants, velocity, predation pressure, aquatic vegetation, or presence of *Microcystis* in a regular spatial and temporal frame. Data on several of these variables do exist, but not in time series or in data sets that cover the geographic range of delta smelt. Plainly, as agency managers take stock of the existing data collection scheme, they should seek to gather data – even at limited spatial or temporal scales – regarding these variables that could affect the quality and quantity of available habitat.

Affinity Analyses

Affinity analysis compares the availability of an environmental resource, or physical characteristic or its condition, with the use of that resource or co-occurrence with that physical characteristic by a target species (Lechowicz 1982, Grost et al. 1990, Monaco et al. 1998, Cardona 2006). When little is known about a species, an affinity analysis can offer

insights into the nature of the relationship between an environmental attribute and the target species, depending on whether the species exhibits an affinity with or aversion to the environmental attribute, and whether an affinity, if found, is strong or weak. It does not require the *a priori* specification of a functional ecological relationship; therefore, it does not presuppose the nature of the relationship that may exist. Graphical depictions of the results can assist in identifying threshold phenomena and other non-linear relationships that may be inherent to the fish-factor interaction. In utilizing an affinity analysis approach, care must be taken to consider collinearity between variables, as well as appropriate segmentation of the attribute range in depictions of continuous data.

The environmental attributes that appeared to be pertinent and that met data-adequacy criteria for inclusion in the affinity analysis (from Table 1) were turbidity, salinity, temperature, food availability, channel depth, channel width, water body type, area of shallow water, proximity to wetlands, and substrate during spawning.

In conducting the affinity analyses, we divided the full range of data for each attribute into 6 to 9 segments (or increments). The delineation of the segments reflected the nature of the attribute considered. The segments were generally of equal magnitude through the range of delta smelt occurrences for turbidity and depth. For temperature, the magnitudes of some segments were narrowed to provide more detailed information for the response variable (for example, temperatures during summer that might induce stress). For other attributes, including salinity, turbidity, prey density, channel depth, area of shallows, and distance to wetlands, the delineation of segments reflected a near-exponential increment

spacing. Other delineations reflected discrete categories of the attribute (for water body type and substrate).

For each monitoring-program month during which a targeted life stage was abundant (that defined here as exceeding 10% of the annual total of individuals sampled), we used pivot tables (in Microsoft Excel) to enumerate the number of delta smelt individuals and the number of observations in each attribute segment. We then converted each of those to a percentage value for each month, and generated summary statistics across months and years to produce statistics on the average percentage of availability for each attribute segment, the average use of each segment, the average difference between the two, and the standard deviations of each to determine a 90% confidence interval.

We present affinity analyses as graphs for each life stage showing the percentage distribution of delta smelt across a segmented attribute range compared to the availability of the resource. We display the difference between resource availability and its use, along with the 90% confidence interval surrounding the difference. These graphics appear in supplementary material to this paper.

Derivation of Suitability Indices

It has been frequent practice to present the value of an environmental attribute to a species in a habitat suitability index, as demonstrated by its application to more than 50 fish species

http://el.erdc.usace.army.mil/emrrp/emris/emrishelp3/list_of_habitat_suitability_index_hsi_models_pac.htm). Suitability indices are hypothetical models, which are typically developed from a review and synthesis of existing information on the established use of a resource by that species. The relationship is scaled to produce an index of habitat suitability on a scale between 0 (unsuitable habitat) and 1 (optimally suitable habitat) (see Weinstein 1986). Guay et al. (2000) utilized affinity studies to develop suitability indices for juvenile Atlantic salmon, which they referred to as “preference indexes.” We largely follow that approach by employing average use-to-availability ratios across months and years for each attribute segment and life stage to assess environmental factor suitability for delta smelt. But Guay and his colleagues utilized the maximum score from the use-to-availability ratio to scale remaining ratios in other segments, while we used the ratio of the use to availability of a habitat attribute or 1, whichever was less, in an attempt to differentiate suitable environmental attribute ranges (that is, those with a suitability index values equaling 1) from ranges less suitable. In so doing, we recognize that expressed preference or aversion by a species to a specific environmental factor and condition is relative – individuals may actually inhabit a location because conditions there are “better” than at alternative locations, not necessarily because the location offers environmental conditions that might be described as optimal, good, or even adequate. Rather than producing peaked functions similar to those presented by Guay et al., our approach produces an attenuated (flatter) response, more representative of the response functions that might be inferred from historical distributions of fish and environmental conditions in the Delta (Pardue 1983, Weinstein 1986, Stier and Crance 1985). To obtain values for the

entire range of an attribute with continuous values, we used linear interpolation between the index values at the midpoints of each segment.

Development of numerical indexes for habitat quality

An indication of the overall suitability of prevailing environmental conditions for delta smelt at any geographic location (l) and any point in time (t) may be derived by calculating a Habitat Suitability Index (HSI), which is the geometric mean of suitability indices for multiple individual attributes (S_i) (Brown et al. 2000, Guay et al. 2000), with:

$$HSI_{lt} = \prod S_{ilt}$$

HSI values can then be aggregated over space and time to enumerate the quality of habit in a region or over time. We believe the multiplicative nature of this model is appropriate and important. A multiplicative, rather than additive model provides that any one attribute, if at a sufficiently bad level will cause the HSI score to be close to zero. For example, a site with water that at lethal temperatures will be uninhabitable, even if there is ample food.

To allow for the possibility that habitat attributes may not be of equal importance in determining habitat quality, we followed the approach of Guay et al. (2000), and specified a functional form utilizing a weighted geometric mean of attributes, offered as:

$$HSI_{lt} = \alpha \prod S_{ilt}^{\beta_i}$$

We calculated the weights, β_i , by regressing the suitability values in log form against the log of the percentage of delta smelt at a given survey station. A value of 0.01 was added to time series that included zero values to allow logarithmic calculation. We chose to use the relative distribution of delta smelt, rather than absolute densities, to correct for inter-annual variation in abundances. We use the results of the multiple regression analysis both to identify significant attributes and to calculate a weighted HSI for each observation.

Spatial Depictions

Having identified environmental variables that appear to influence the distribution of delta smelt, the final element of the study was to identify how frequently environmental attributes occur in ranges that may be less than adequate, and where these circumstances occur, to suggest an appropriate type of restoration activity and location for a next level of management planning consideration.

We calculated the frequency with which attributes were less than adequate (that is, exhibited suitability index values in an aversion range) for salinity, turbidity, temperature, and prey density. We also identified locations where water depth was considered less than adequate (using estuary-wide bathymetric data) or where wetlands could be considered too distant. This enabled us to identify areas for potential channel modification and wetlands restoration. We developed criteria for candidate restoration sites where elevations approximate sea level (to utilize tidal processes without undue earthwork) or

areas where other environmental attributes frequently occur in adequate ranges (to increase the likelihood of use by the species). We did not attempt to evaluate any potential sites in Suisun Marsh, because we do not have the detailed understanding of the hydraulic connectivity between tidal marshlands and main channels that is needed for rigorous evaluation.

On terminology

Acknowledging that the *de rigueur* terms used to convey “preferences” by organisms for essential resources, other environmental attributes, and landscape circumstances tend to default to value judgments -- environmental conditions are sometimes described as “optimal,” or as near anthropomorphisms, wherein conditions are often referred to as “desirable” -- we have restricted this presentation to a purposefully neutral terminology. We describe delta smelt as showing *strong affinity* or *strong aversion* for environmental attribute conditions where survey returns indicate that the difference between delta smelt occurrences in a range segment and availability of that range segment in the estuary is significantly different from zero at the 90% level of confidence. Environmental conditions in areas to which delta smelt show strong affinity are considered *suitable*; conditions where delta smelt exhibit a strong aversion are *inadequate*. Where delta smelt exhibit weak affinity, areas are referred to as *adequate*.

RESULTS

Affinity Analyses

Delta smelt associations with seven environmental attributes of (or resources in) the estuary for five life stages during six sampling periods are presented as ranges of conditions in Table 4 and as histograms in Supplementary Figures S1-S7. These seven attributes can be inferred to contribute to delta smelt habitat – turbidity, salinity, temperature, food availability, sub-surface depth, extent of shallow water, and distance to large wetlands. Affinity studies for water body type, water body width, and substrate at spawning revealed no notable relationships that appear to inform habitat restoration. Delta smelt life stages are described as expressing affinity for a range of conditions for each environmental attribute, where the attribute or resource use or co-occurrence (the height of the red column in the supplementary histograms) exceeds that of relative attribute or resource availability (the height of the blue column with which it is paired). Delta smelt are averse to circumstances in which that relationship is reversed. Differences between the paired columns are depicted with green dots bracketed by a 90% confidence interval and referenced by the right axis. Life stage-specific affinities and aversions for the suite of environmental attribute conditions can be summed to shape a multi-dimensional description of delta smelt habitat, which can be used to inform habitat restoration efforts targeting delta smelt. A multi-dimensional “habitat space” emerges from pairing distribution data for each delta smelt life stage, with temporally appropriate data on each environmental attribute.

Sub-juvenile delta smelt are sampled while dispersing from shallow spawning areas to the open water areas in which they then feed and grow. Having less-developed swimming abilities, they do not express associations with environmental attributes as closely as they appear to in later life stages. Sub-juveniles do express a strong affinity for moderate turbidity (20-40 cm) (Figure S1a). And, while sub-juveniles are frequently found in near-freshwater conditions typical of spawning areas (Figure S2a), they are tolerant of salinities up to 4000 Ec. Water temperatures are rarely in the ranges that might induce stress in this life stage, but sub-juveniles seem to avoid waters in excess of 22 degrees C (Figure S3a). No consistent pattern of sub-juvenile distribution emerges across the range of bathymetric characteristics in the estuary, although strong affinity exists for water deeper than 7m (Figure S5a), and at least a limited area (5-20 ha) of shallow-water circumstances (Figure S6a). A requirement for channel complexity – essentially deep channels that meander through tidal marshlands – presumably is consistent with conditions that were present in the pre- settlement estuary. No strong affinity is expressed by sub-juveniles for prey density (Figure S4a), perhaps reflecting two factors -- sub-juveniles are a life stage in transit, and there may be a complex interaction between prey and predators that affects copepod densities, which is poorly accounted for in the available data. While a strong affinity by delta smelt for areas supporting greater prey density is not demonstrated, there is an affinity for areas in (close) proximity to wetlands (Figure S7a), which becomes more evident in later life stages.

For *juvenile delta smelt*, a strong affinity exists for turbid water less than 40cm Secchi depth (Figure S1b and S2c). Juveniles demonstrate an affinity for waters with salinity up to 8000 Ec (Figures S2b and S2c). They exhibit a strong aversion to water greater than 22 degrees C and are rarely found in circumstances exceeding 23 degrees C (Figures S3b and S3c). An affinity for water depth more than 7 m (Figure S5b and S5c) and for adjacent shallow areas exceeding 100 ha in extent is apparent (Figures S6b and S6c). The primary area where this suitable condition occurs is in Grizzly Bay; a large area of shallow water into which (presumably) nutrient-rich water from Montezuma Slough empties, providing a food source to a life stage with a not yet fully developed swimming capacity. An affinity for prey densities exceeding 250 individual copepods per m³ is pronounced in juvenile delta smelt (Figure S4b), as is an affinity for areas within 2 km of wetlands (Figure S7b and S7c). Juveniles appear to express a strong aversion for locations that support high prey densities -- likely an anomaly reflecting the presence of higher prey densities in the south Delta at times when prevailing turbidity or temperature conditions there limit occupancy by delta smelt.

Sub-adult delta smelt appear to be tolerant of a wider range of environmental conditions than earlier stages, likely due to the need for that life stage to cope with variability in several environmental attributes in autumn in the estuary. For example, sub-adults are more tolerant of clear water (Figure S1) and fresh water (Figure S2). They exhibit a weak affinity for salinities up to 8000 Ec, not expressing strong aversion until salinity exceeds 20000 Ec (Figure S2d), twice the salinity level at which aversion is shown by juveniles. Few sub-adults are found in water exceeding 23 degrees C (Figure S3d). Sub-adults show a

strong affinity for water 7-9 m in depth (Figure S5d) and for situations where limited shallow water areas (5-20 ha) exist nearby (Figure S6d), reflecting a continuing association with complex bathymetry. A strong affinity for prey density is not exhibited by sub-adult delta smelt until copepod density exceeds 1000 per m^3 (Figure S4d), perhaps reflecting increased food requirements at this life stage. Sub-adults are found close to larger wetland areas, with strong affinities expressed for locations less than 2km from them (Figure S7d).

The *pre-spawning adult delta smelt* that are found predominately in survey samples taken in January and February, are presumably taken while dispersing to spawning areas (Hamilton and Murphy in press). While they exhibit affinities and aversions, few are as strong as displayed by other life stages. An affinity for turbidity is exhibited in the 20-30 cm Secchi-depth range segment (Figure S1e). The affinity range for salinity is 1000 to 8000 Ec (Figure S2e), with an aversion to freshwater (that is, less than 200 Ec). There appears to be no influence of water temperature on the distribution of pre-spawning adults (Figure S3e). Affinity exists for situations adjacent to limited shallow water circumstances (5-20 ha) (Figure S6e). An affinity for depth conditions appears shift to waters 5 to 6 m deep (Figure S5e), perhaps reflecting dispersal to spawning areas in shallower situations. Pre-spawning adults express an affinity for locations with densities of copepods in the range of 250 to 1000 / m^3 , which is an affinity range lower than observed in previous life stages but locations with copepods at 1000/ m^3 are rare at this time of the year (hence pre-spawning adults exhibit an affinity for the highest prey densities available). An affinity for locations in proximity to wetlands is strong; highest with wetlands in the range of less than 250

meters distant (Figure S7e), suggesting that wetlands may not only be important for food production, but that they also provide some essential conditions for reproduction.

Spawning adults sampled in trawl surveys number the fewest of all life stages. Since the reduction in abundance from pre-spawning to spawning adults is far greater than would be expected due to natural attrition, it is likely that the spawning adults are moving away from the monitoring sites. The few spawners sampled and the truncated duration of the Spring Kodiak Trawl makes it difficult to identify the range of suitable environmental attributes, and, as with other fishes, it might be assumed that spawning areas exhibit attribute conditions that are suitable for the eggs and larvae to come. Spawning adults do express strong affinity for turbid water (20-30 cm Secchi depth), and avoid clear water (greater than 50 cm Secchi depth) (Figure S1f). Interestingly, spawning adults exhibit an aversion to very fresh water (Ec less than 200) (Figure S2f) despite the common description of spawning adults as moving to fresh water to spawn. As with pre-spawning adults, temperature seems to play no apparent role in the distribution of fish at this life stage (Figure S3f); likewise the area of shallow water seems to have no bearing on distribution (Figure S6f), although there is an association with water 5 to 6 meters deep (Figure S5f). Spawning adults avoid areas with little food ($<100/m^3$) (Figure S4f), and express an affinity for waters within 0.25 km and 1 to 2 km of large wetlands (Figure S7f).

Habitat Suitability

Given the purpose of this study -- to identify areas that should benefit from restoration efforts targeting delta smelt and to identify particular management actions at specific sites -- we focus on the areas where physical and biotic conditions are frequently unsuitable, allowing planners to exclude those areas, and in so doing, identify residual areas that may be suitable for physical and biological restoration actions.

Maps illustrating the distribution of categorical environmental variable conditions – turbidity, salinity, temperature, prey density, water depth, extent of shallow water, and distance to large wetlands (Figures 2-13) -- illustrate in a spatially explicit format the extent to which sub-areas of the estuary are inadequate or unsuitable for delta smelt (and see Table 4 for supporting range values).

The habitat suitability index curves for turbidity (Figure S8) depict a generally consistent relationship for all life stages: water with a Secchi depth of 10 to 35 cm represents suitable habitat; that range can be extended up to 55 cm Secchi depth in the fall when the adults begin to move to spawning areas. During June and July, the water in the central and south Delta frequently exhibits Secchi depth greater than 50 cm, making much of that area too clear (not sufficiently turbid) to be suitable for delta smelt (Figure 2). At the same time conditions in the area from Liberty Island, east and up the lower Sacramento River, and west in the lower Napa River rarely experience unsuitable turbidity conditions. In the fall, areas of the estuary with turbidity frequently in a suitable range are reduced in extent (Figure 3), with suitable turbidities frequently being found only in the northern portion of

Suisun Bay, Montezuma Slough, areas around the Sacramento-San Joaquin rivers confluence, and the Sacramento ship channel.

Very fresh water (that is, water less than 200 Ec) is not suitable for any life stage of delta smelt, but delta smelt are found in a wide range of salinities (Figure S9), with the range varying by life stage. Subjuveniles occur in salinity of up to 4,000 Ec; suitable conditions for juveniles includes salinities up to 8,000 Ec, for sub-adults up to 12,000 Ec, and spawning and pre-spawning adults up to 8,000 Ec. Consequently, the estuary can be too fresh in certain places (Figures 4 and 5) and too saline in other places (Figures 6 and 7) to be suitable for delta smelt. Between these limits in the west and east extremes of the estuary, delta smelt persist in diverse circumstances. Suisun Bay and Montezuma Slough rarely experience water conditions that are too fresh in June and July, whereas the lower Sacramento River and lower San Joaquin River, upstream of the confluence with Old River, frequently experience water that may be too fresh for delta smelt (Figure 4). In the fall, only the north Delta above Rio Vista and the east Delta offer conditions that may be too fresh for delta smelt (Figure 5). In June and July, water conditions in the far western portion of Suisun Bay can be too saline, hence not suitable for delta smelt (Figure 6). Salinity levels increase in the fall, but the tolerance of then-older delta smelt to salinity also appears to increase. The net effect is that a portion of western Suisun Bay may be too saline to be suitable for delta smelt (Figure 7).

Delta smelt exist in open water up to 22 degrees C, beyond which suitability decreases quickly (Figure S10). Temperatures greater than 22 degrees C are common in the south Delta during June and July (Figure 8).

Suitability index curves for prey density (Figure S11) do not indicate that sub-juveniles alter their position in the estuary in relation to prey density. As the fish mature, more frequent delta smelt occurrences are associated with higher prey densities. Habitat for juvenile and older life stages appears to require prey densities exceeding 250/m³. Average prey density does not correlate well with the average distribution of delta smelt, suggesting that prey availability and delta smelt occurrences should not be considered on a coincident temporal basis. That noted, there are areas within the Delta that frequently exhibit prey at densities sufficient to provide suitable habitat for delta smelt. Copepod densities in June and July are highest in the south Delta (Figure 9), but these areas frequently have other attributes in ranges that are unsuitable for delta smelt. But areas of the central Delta with frequently higher prey densities exist. Conversely, there are areas within the Delta typically inhabited by delta smelt that are frequently food limited; moreover data suggest that wide areas of the estuary exhibit limitations on food availability in the fall (Figure 10).

The depth requirements for delta smelt occupancy appear to differ during the species' life history and reflect an aversion to both shallow- and deep-water circumstances during much of the species' life cycle. Delta smelt express strong affinities for waters of certain depths, 50% of juveniles and sub-adults are found in water 7 to 9 meters deep from July through November. And yet, in early July, delta smelt show strong aversions for water just

a couple of meters shallower; resulting in suitability index curves that are somewhat U-shaped for sub-juveniles and juveniles (Figure S12). Channels in north Suisun Bay and Montezuma Slough include sites with high densities of delta smelt, but also extensive channels with insufficient depth (Figure 11).

The affinity results for areas of shallow water suggest that, for most delta smelt life stages, the presence of at least limited areas of shallow water is an important element of habitat. More than half of delta smelt sampled, from juveniles in the summer through to pre-spawning adults in the winter, are drawn from areas with 5 ha to 20 ha of shallow water within one kilometer of the survey site (Figure S13). While the availability of such circumstances is common in the estuary (Figure 12), some areas could benefit from targeted rehabilitation for that attribute. Such projects may be readily and efficiently combined with wetland restoration efforts to provide significant landscape modification.

The affinity studies identified proximity to large wetlands as an important determinant of delta smelt occupancy of open water circumstances. Suitability index curves (Figure S14) show elevated occupancy by multiple life stages in areas of open water up to 4 km from emergent wetlands. For sub-adults and pre-spawning adults the criterion is 2 km.

Although extensive wetlands are widely distributed throughout Suisun Bay, Suisun Marsh, and adjoining waters, they are sparsely distributed and limited in extent throughout most of the rest of the estuary (Figure 13).

Significance of environmental attributes

The maps that depict the frequency with which individual physical and biotic attributes are inadequate indicate that the estuary is both spatially and temporally complex and variable. In an effort to determine those environmental attributes that may be relevant in restoration planning – versus those that may essentially be redundant – in a multivariate context, we first derived suitability index curves (presented in supplementary figures S8-S14) from the results of the affinity analyses (Figures S1-S7). Next, we regressed the suitability index values for the seven habitat attributes against the relative distribution of delta smelt.

When prey density is excluded from the analysis, the results indicate that turbidity, salinity, and average water depth influence the distribution of delta smelt at all life stages (Table 5). Temperature is a significant determinant of distribution for sub-juvenile and juvenile life stages. Distance to wetlands is significant at juvenile and sub-adult life stages. The area of shallow-water circumstances is significant for juveniles in mid summer (based on Summer Tow-net survey data) and for pre-spawning and spawning adults.

When copepod prey density is included in the analysis (Table 6), prey density is significant only for the juvenile life stage during June and July (based on 20mm data), and the pre-spawning life stage. The coefficient for prey density has a negative sign for sub-juveniles and sub-adults, possibly due to collinearity with other variables. Turbidity is significant at all life stages. Salinity is significant at all but the spawning life stage. Average depth, temperature, and distance to larger wetlands (> 100 ha) are significant for sub-juvenile,

juvenile and sub-adult life stages. Area of shallows is significant for juveniles in mid summer (based on Summer Tow-net Survey data) and for pre-spawning adults.

To identify landscape areas that are most likely to host successful restoration programs, we summarize the water quality attributes (turbidity, salinity and temperature) into an average HSI for each station. The HSI was derived from a weighted geometric mean of the suitability index values for the attributes, utilizing the coefficients from Table 5 as the weights. We depicted the average value for each station geographically both for juveniles in the 20 mm Survey (Figure 14) and pre-spawning adults in the Spring Kodiak trawl (Figure 15). These figures indicate that areas in the vicinity of Suisun Marsh, at the confluence of the Sacramento and San Joaquin rivers and in the north Delta have the highest geometrically weighted average HSI values for water-quality environmental attributes, and should be viewed as representing potential priority target areas for habitat restoration efforts.

Restoration Guidance

The results presented in Tables 5 and 6 indicate that modification of channel depth or restoration of emergent wetlands (tidal marsh, freshwater marsh, and riparian strands) could substantively improve the suitability of environmental conditions for delta smelt at locations where other environmental attributes are frequently in suitable ranges. The geographic distribution of areas that are most likely to benefit delta smelt from environmental restoration (habitat improvement) efforts is provided in Figure 15. We suggest that these types of maps (at finer resolution) can assist in establishing priorities for

early-term projects where habitat suitability for delta smelt can be enhanced through improvement focused on a select environmental attribute. Examples of potential project sites in priority target areas are presented in Figure 16 (for channel modification and wetlands restoration).

DISCUSSION

Survey returns for multiple life stages of delta smelt were analyzed with time-series data for several environmental factors that contribute to the extent and quality of its habitat in an effort to provide guidance to planned restoration efforts, including those under the ambitious Bay-Delta Conservation Plan. The physical and biotic conditions associated with delta smelt presence are multi-dimensional and the suitability of environmental attribute conditions vary with life stage. Based on analyses using trawl survey data, delta smelt demonstrate an affinity for certain environmental conditions that differ significantly from the frequency with which those conditions occur in the estuary. Delta smelt occupy a continuum of suitable areas of the estuary, and appear to avoid (are averse to) areas of the estuary with environmental attributes in less than adequate ranges. The affinity analyses indicate that different portions of the Delta exhibit diverse conditions for seven environmental variables that contribute to habitat extent and quality for delta smelt. Different sub-regions of the estuary and local areas within those sub-regions vary in their suitability for delta smelt, and do so in discordant patterns.

The results from the analyses in this study facilitate identification of areas of the Delta that experience ranges of environmental conditions that are acceptable and unacceptable to delta smelt. Maps of the distribution of delta smelt in the estuary offer insights into delta smelt habitat requirements, suggesting that environmental (factor) suitability exists on two spatial scales that are salient to planning for habitat restoration. At a broad geographic scale, from many kilometers to the entire Delta, patterns of spatial variation in water-quality factors indicate that large areas of the estuary, especially in south and southeast Delta are frequently unsuitable for delta smelt. At a narrower geographic scale, several kilometers and below, and within Delta areas that experience water-quality conditions that very frequently are suitable for delta smelt, site-specific differences in water-body and channel morphology, and proximity to emergent wetlands, offer a mechanistic explanation for contemporary patterns of delta smelt distribution. Considering both spatial scales in restoration project site selection and prioritization should enhance the prospects for success in establishing or reestablishing delta smelt occupancy in new or formerly occupied areas of the Delta.

Three factors related to water quality -- turbidity, salinity, and temperature -- while alone not competent to characterize the habitat space available to delta smelt, contribute to defining the spaces available for habitat restoration actions targeting delta smelt (see Bennett 2005). Where one or more of these factors frequently fall outside of the range suitable for delta smelt, habitat restoration efforts are likely to fail to provide the full complement of ecological conditions necessary to support delta smelt. In the summer and fall, as delta smelt are feeding and growing in anticipation of spawning, the fish's range in

the estuary is located between water that is too saline in the west (west of Suisun Bay) and too fresh in the east (in the lower Sacramento River near and north of Rio Vista, and south across the Cosumnes, Mokelumne, and San Joaquin rivers inputs to the estuary), essentially the entire tidally influenced Delta, along with the lower Napa River (Merz et al. 2012, Murphy and Hamilton 2013). Salinity constrains delta smelt to the Sacramento-San Joaquin Delta and adjacent Suisun Bay and Suisun Marsh, but only to the extent that a portion of western Suisun Bay may not provide suitable salinity conditions in low Delta-outflow circumstances, especially late in very dry years; and, areas that experience purely freshwater circumstances above Sacramento on the Sacramento River appear not to be consistently occupied by delta smelt.

While habitat restoration efforts targeting delta smelt, therefore, largely appear not to be geographically constrained by salinity conditions, inter-seasonal turbidity and temperature regimes serve to differentiate the low-salinity zone of the Delta into areas that are often occupied and can be occupied by delta smelt, and areas that experience conditions adverse to the fish. Southern and eastern portions of the estuary are frequently too clear in the fall and too warm in the summer to provide year-round habitat for delta smelt, even if other physical and biotic conditions are suitable for the fish. The finding that water clarity frequently is too high (turbidity too low) and water temperature too high in certain areas should steer habitat restoration planning and actions to elsewhere in the Delta. In addition, neither turbidity nor temperature can be readily addressed through targeted management actions in the estuary -- for example, reduced turbidity in the San Joaquin River and southeastern estuary in part may be resulting from sediment impoundments behind

tributary dams and hardened river channels that are located far from the conservation planning area. Therefore, for purposes of near-term conservation planning, those areas should be at best low-priority sites for delta smelt habitat restoration. Furthermore, anticipated trends in environmental factor conditions may render additional portions of the estuary unsuitable for delta smelt; for example, water temperatures in the estuary can be anticipated to rise, expanding the footprint of conditions that are unsuitable for the fish (see Cloern et al. 2011). Nonetheless, a wide swath of the estuary, from Suisun Bay and Suisun Marsh in the west to Cache Slough and the Sacramento ship channel in the east, appears to consistently experience turbidity and temperature conditions suitable for delta smelt.

The physical and biotic conditions required for delta smelt presence, which collectively serve as a proxy for delta smelt habitat, are multi-dimensional. The findings presented here indicate that habitat restoration efforts for delta smelt must consider, on the one hand, the broad ranges in, and geographic patterns exhibited by, water turbidity, salinity and temperature conditions, which vary by life stage; and, on the other hand, the availability of adequate supplies of its copepod prey, the presence of which at least in part is determined by landscape conditions. The trophic linkages between the production of the phytoplankton that serve as the primary foods for the zooplankton (copepods) that are the primary prey of delta smelt are well established (Kimmerer and Orsi 1996, Nobriga 1998). And, the clear relationships between wetlands and primary productivity in adjacent waters (see Alpine and Cloern 1992) has prompted a generally recognized need for ecosystem rehabilitation at the land-estuary interface to enhance the “production, transport, and

transformation of organic matter that constitutes the primary food supply to the base of the food web” (Jassby and Cloern 2000). Although “the production and distribution of phytoplankton can be highly variable within and between nearby habitats of the same type, due to phytoplankton sources, sinks, and transport” (Lucas et al. 2002), the restoration of tidal wetlands has been identified as the primary means for enhancing habitat for delta smelt (BDCP 2013). Combine the findings from the habitat affinity analyses for channel (or embayment) depth, area of adjacent shallow circumstances, and distance to emergent wetlands, and a target condition for site-specific habitat restoration emerges. Delta smelt show an affinity for areas with heterogeneous bathymetry where deep channels are found in proximity to shallower circumstances and emergent wetlands, the latter land-cover type providing for greater primary production and abundance of prey used by delta smelt.

Conservation planners seeking to implement projects that have higher likelihoods of success in producing habitat conditions that are associated with delta smelt presence might view higher-priority projects as those that fall within the existing geographic range of delta smelt and require minimal redirection of resources available for conservation. The copepod prey that supports delta smelt frequently appears to be limiting in early summer in a number of locations in the northern portions of the estuary, and in Napa River and its estuary, especially in autumn months. It is likely that targeted tidal marsh and freshwater marsh restoration (and creation) in northern portions of the estuary would serve to enhance the availability of food, as well as access to spawning areas. More specifically, it appears that restoration of large emergent wetlands in eastern Montezuma Slough, the Sacramento River below Isleton, and the Cache Slough area could improve habitat

availability and conditions for delta smelt. Furthermore, it appears that habitat conditions in areas in north Suisun Bay and Montezuma Slough could be improved with channel modifications; and, increasing the availability of areas of shallow water in Grizzly Bay, Suisun Bay, and some stretches of the lower Sacramento River could improve habitat in those areas for young delta smelt.

The results of the affinity analyses presented here appear to have immediate application. The proposal to restore habitat for delta smelt in the BDCP is embedded in a conservation strategy that follows a biological opinion produced by the U.S. Fish and Wildlife Service in 2008, which determined that ongoing water export operations from the estuary by state and federal pumping projects likely jeopardize the continued existence of the delta smelt. While recognizing that a broad array of physical and biotic factors provide essential resources and contribute to habitat for delta smelt, the Service chose to use the location of the low-salinity zone in the estuary as a surrogate measure of the extent and quality of habitat for delta smelt. The BDCP is following the agency lead by employing the extent of the low-salinity zone, which expands during periods of high outflow through the estuary, as proxy for the summed environmental attributes that must co-occur to allow for the presence delta smelt. The plan concludes that increased suitable habitat for delta smelt becomes available when the lower-salinity portions of the Delta's low-salinity zone is particularly expansive, and it measures benefits to delta smelt and program success as a function of a salinity-habitat relationship (BDCP 2013). But, the mapped analyses presented here illustrate potential trade-offs that may be important in restoration planning decisions. For example, water management decisions that contribute to shifting the

location of the low-salinity zone in the Delta to the west (downstream, as proscribed under certain “water-year” circumstances in a recent delta smelt biological opinion [USFWS 2008]) may improve habitat conditions in some parts of the estuary, but at the same time render other areas less suitable or unsuitable to delta smelt during portions of the year.

The location and extent of the low-salinity zone in the estuary is a “coarse filter” (see Noon, et al. 2007) for purposes of conservation planning for delta smelt; providing little guidance to site-specific restoration efforts beyond setting wide bounds on the estuary landscape within which directed management actions should occur. As the maps accompanying the affinity analysis clearly indicate, the location of the low-salinity zone is a weak predictor of the presence of delta smelt at the scale that habitat restoration for the species will be carried out. In the zone where delta are currently found, landscape cover and bathymetric factors appear to be the best predictors of the presence of delta smelt and may be the most effective surrogate environmental attributes for, or environmental indicators of, habitat for delta smelt habitat.

The validity of these findings is, of course, related to the reliability of the survey data on delta smelt and the accompanying environmental variables upon which the affinity analysis was based. The longer time-series data sets on delta smelt that were used in this study are derived from trawler-based surveys of fishes taken from the estuary’s open waters; few samples in shorter time-series are available from across the bathymetric gradient occupied by delta smelt. Water-quality data were taken concurrently with fish samples, hence are similarly limited. Zooplankton samples are largely collected independently, and suffer from

degrees of spatial and temporal discordance with delta smelt samples. Both the fish survey and environmental factor data sets are derived from studies that unfortunately are limited in geographic footprint, missing data from essential geographic locations on the estuary's periphery, where range limits of environmental attributes are commonplace. These shortcomings in the database for the estuary will need to be rectified in any performance measure-based monitoring efforts that are developed to accompany restoration efforts. But, given the ambitions of this study and its accompanying information needs, the extent and resolution of the data might fairly be viewed as adequate. At the same time, the urgency for restoration actions within the estuary to facilitate the recovery of protected native fishes cannot wait for improved monitoring programs -- restoration must proceed utilizing the best currently available data.

The absence of well-resolved environmental variables, beyond the seven used in the habitat affinity analyses carried out here, has implications to restoration planning. Geographic patterns of predation on delta smelt are not known, but the marsh-edge conditions to which delta smelt show a strong affinity host high-densities of non-native fish species, many of them documented to prey on delta smelt (Feyrer 2004, Sommer et al. 2004). Cohen and Carleton (1998) found in the San Francisco estuary up to 97% of the total number of organisms and 99% of the biomass to be alien invasive species, leading Grimaldo et al. (2004) to opine that management efforts should "create or restore wetlands that only flood during winter and spring, the period when native fishes spawn and recruit into the estuary." Clearly restoration actions that might benefit predators over the imperiled delta smelt should be avoided.

Contaminant loading is a lead concern in the conservation of delta smelt and other native fish species in the Delta and adjacent areas of the estuary. Concerning the latter, one contaminant that has been recorded in ecologically relevant concentrations in areas occupied by delta smelt is ammonium. It is released from municipal wastewater treatment facilities, creates imbalances in nitrogen-phosphorus ratios and contributes to increases in chemically reduced nitrogen concentrations that impair primary productivity (Dugdale et al 2007) and is associated with food web disruption, including reduced availability of diatom species that serve as prey for the zooplankton upon which delta smelt depend (Glibert et al 2011). Changes in nutrient ratios and nutrient concentrations, which are correlated with elevated ammonium, create conditions conducive to invasions of rooted aquatic vegetation, toxic blue-green algae, and bi-valve mollusks (Glibert et al 2011), all habitat quality-compromising stressors that are thought to have direct and indirect deleterious effects on delta smelt abundance. Otherwise well-crafted restoration efforts in locations that could be expected to support delta smelt, could well fail or under perform due to local contaminant conditions that could not be considered in this study.

Environmental variables in addition to those addressed in this habitat affinity analysis need to be considered by restoration planners before location-specific actions are taken. But, the approach taken here in assessing estuary conditions for delta smelt uses environmental variables on water quality, food availability, morphological water-body and channel characteristics, and proximity to wetlands to effectively describe the multidimensional space that supports much of the current distribution of multiple delta

smelt life stages. Using a diversity of estuary attributes in the affinity analysis allows for a comprehensive characterization of conditions that are acceptable, and conversely appear to be undesirable, to delta smelt. The environmental variables considered here shed light on resource conditions that appear to determine the presence and absence of delta smelt at a range of spatial scales. Guidance that can be gleaned from this study for future environmental restoration efforts targeting delta smelt includes, not just identification of areas of the estuary that should be avoided because they are unlikely to support delta smelt regardless of restoration actions, but also direction toward areas where actions are likely to succeed in enhancing delta smelt productivity, and identification of the restoration and enhancement measures necessary to generate and sustain that productivity. This study can be used as a helpmate in identifying and locating candidate restoration actions; where preferred or highest-priority projects are those that fall within the existing geographic range of delta smelt, require minimal redirection of other resources, and can be implemented where the geographic extent of actions needed is limited – in other words, where more focused restoration efforts targeting fewer environmental attributes (habitat factors) are addressed on landscape areas adjacent to locations that already support delta smelt.

That recommendation married with spatially explicit observations from the affinity analyses and mapped data can form the foundation for a strategic approach to restoration site selection and site-specific management planning. All restoration projects require direct engagement of resources, frequently redirection of resources away from other beneficial applications, which inevitably has both ecological and economic consequences. In that light

we believe it would not be prudent to invest in restoration actions in areas that are determined now or projected to be deleteriously impacted in the future by water quality variables that fall out of the range of suitability for delta smelt. The creation of habitat, or the restoration of areas that exhibit attributes within affinity ranges for delta smelt (but are currently unsuitable) inside the contemporary range of the fish, should be those most likely to contribute to enhancing the fish's productivity and recovery.

Literature Cited

- Alpine, A.E. and J.E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946-955.
- Armor, C., R. Baxter, W. Bennett, R. Breuer, M. Chotkowski, P. Coulston, D. Denton, B. Herbold, W. Kimmerer, K. Larsen, M. Nobriga, K. Rose, T. Sommer, and M. Stacey. 2005. Interagency Ecological Program Synthesis of 2005 Work to Evaluate the Pelagic Organism Decline (POD) in the Upper San Francisco Estuary. Interagency Ecological Program. Available online at: http://www.science.calwater.ca.gov/pdf/workshops/POD/2005 IEPPOD synthesis report_111405.pdf
- Bajer, P.G. and M.L. Wildhaber. 2007. Population viability analysis of lower Missouri river shovelnose sturgeon with initial application to the pallid sturgeon. *Journal of Applied Ichthyology* 23:457-464.
- Baskerville-Bridges, B., J. Lindberg, and S.I. Doroshov. 2004. The effect of light intensity, alga concentration, and prey density on the feeding behavior of delta smelt *Hypomesus transpacificus* larvae. In: Feyrer F., L.R. Brown LR, R.L. Brown, J.J. Orsi, editors. *Early Life History of Fishes in the San Francisco Estuary and Watershed*. Bethesda (MD): American Fisheries Society Symposium 39: 219-228.
- Baxter, R., R. Breuer, L. Brown, M. Chotkowski, F. Feyrer, M. Gingras, B. Herbold, A. Mueller-Solger, M. Nobriga, T. Sommer, and K. Souza. 2008. Pelagic Organism Decline Progress Report: 2007 Synthesis of Results. Available online at: http://www.science.calwater.ca.gov/pdf/workshops/POD/2007 IEPPOD synthesis report_031408.pdf
- BDCP. 2013. <http://baydeltaconservationplan.com/Home.aspx>
- Bennett, W.A. 2005. Critical assessment of the delta smelt population in the San Francisco Estuary, California. *San Francisco Estuary and Watershed Science*. Volume 3, Issue 2 (September), Article 1. Available online at: <http://repositories.cdlib.org/jmie/sfew/s/vol3/iss2/art1>
- Brooks, M.L., E. Fleishman, L.R. Brown, et al. 2012. Life histories, salinity zones, and sublethal contributions of contaminants to pelagic fish declines illustrated with a case study of San Francisco estuary, California, USA. *Estuaries and Coasts*...
- Brown, L.R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* 57: 251-269. Available online at: <http://www.springerlink.com/content/w17n763hl7337802/>

Brown, C.L. and S.N. Luoma 1995. Use of the euryhaline bivalve *Potamocorbula amaurensis* as a biosentinel species to assess trace metal contamination in San Francisco Bay. Marine Ecology Progress. Series 124: 129-142.

Cardona L. 2006. Habitat selection by grey mullets (Osteichthyes: Mugilidae) in Mediterranean estuaries: the role of salinity. *Scientia Marina* 70:443-455.

Available online at:

<http://scientiamarina.revistas.csic.es/index.php/scientiamarina/article/viewArticle/96>

CDWR. 2007. California State Water Project 2006 Watershed Sanitary Survey Update, Final Report, June 2007. Chapter 4 on file (Key concerns in the Central valley Watershed and the Delta).

Cloern, J.E., N. Knowles, L.R. Brown, et al. 2011. Projected evolution of California's San Francisco Bay-Delta-River system in a century of climate change. *PLoS ONE* 6(9): e24465.

Cohen A.N. and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555-558.

Connon, R.E., J. Geist, J. Pfeiff, A.V. Loguinov, L.S. D'Abronzio, H. Wintz, C.D. Vulpe and I. Werner. 2009. Linking mechanistic and behavioral responses to sublethal esfenvalerate exposure in the endangered delta smelt, *Hypomesus transpacificus*. *BMC Genomics* 19:1-18.

Dugdale, R.C., F.P. Wilkerson, V.E. Hogue, and A. Marchi. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuarine, Coastal and Shelf Science* 73: 17-29.

Feyrer F. 2004. Ecological segregation of native and alien larval fish assemblages in the southern Sacramento-San Joaquin Delta. *Early Life History of Fishes in the San Francisco Estuary and Watershed*. American Fisheries Society Symposium 39:67-79. Available online at:

http://swrcb2.swrcb.ca.gov/waterrights/water_issues/programs/bay_delta/wq_control_plans/2006wqcp/exhibits/append2/doi/doi-33d.pdf

Feyrer, F., M. Nobriga, and T. Sommer. 2007. Multi-decadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 136:1393-1405.

Glibert, P.M., D. Fullerton, J.M. Burkholder, J.C. Cornwell, and T.M. Kana. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco estuary and comparative systems. *Reviews in Fisheries Science* 19: 358-417.

Grimaldo, L.F., R.E. Miller, C.M. Peregrin, and Z.P. Hymanson. 2004. Spatial and temporal distribution of ichthyoplankton in three habitat types of the Sacramento-San Joaquin Delta. Pages 81-96 in F. Feyrer, L.R. Brown, R.L. Brown, and J.J. Orsi, editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland. Available online at: [http://www.iep.ca.gov/AES/Grimaldo et al 2004.pdf](http://www.iep.ca.gov/AES/Grimaldo_et_al_2004.pdf)

Grimaldo, L.F., T.R. Sommer, N. Van Ark, G. Jones, E. Holland, P.B. Moyle, P. Smith, and B. Herbold. 2009a. Factors affecting fish entrainment into massive water diversions in a freshwater tidal estuary: can fish losses be managed? North American Journal of Fisheries Management. 29:1253-1270. Available online at: <http://afsjournals.org/doi/abs/10.1577/M08-062.1>

Grimaldo L.F., A.R. Stewart , and W.J. Kimmerer. 2009b. Dietary segregation of pelagic and littoral fish assemblages in a highly modified tidal freshwater estuary. Marine and Coastal Fisheries: Dynamics Management, and Ecosystem Science 1:200–217.

Grost, R.T., W.A. Hubert, and T.A. Wesche. 1990. Redd site selection by brown trout in Douglas Creek, Wyoming. Journal of Freshwater Ecology 5:365-371. Available online at: <http://library.wrds.uwyo.edu/wrp/90-22/90-22.pdf>

Guay J.C., D. Boisclair, D. Rioux, M. Leclerc, M. Lapointe, and P. Legendre. 2000. Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*) Canadian Journal of Aquatic Sciences 57:2065-2075.

Healey, M.C. 2007. Context memorandum: Delta ecosystem. Available online at: [http://deltavision.ca.gov/Context Memos/Environment/Ecosystem Iteration1.pdf](http://deltavision.ca.gov/Context_Memos/Environment/Ecosystem_Iteration1.pdf)

Hieb, K. and K. Fleming. 1999. Summary chapter. In: Orsi, J., editor. Report on the 1980-1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Interagency Ecological Program for the San Francisco Estuary Technical Report 63. 503 p.

Hobbs, J.A., W.A. Bennett, and J.E. Burton. 2006. Assessing nursery habitat quality for native smelts (Osmeridae) in the low-salinity zone of the San Francisco estuary. Journal of Fish Biology 69:907–922.

Jassby and Cloern 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). Aquatic Conservation: Marine and Freshwater Ecosystems 10:323-352.

Johnson, N.K., F. Swanson, M. Herring and S. Greene. 1999. Bioregional assessments: Science at the crossroads of management and policy. Island Press. Covelo, CA.

Karieva, P. M., S. Andelman, D.F. Doak, et al. 1998. Using science in habitat conservation plans. National Center for Ecological Analysis and Synthesis.

Kimmerer, W.J. 2008. Losses of Sacramento River Chinook salmon and delta smelt to entrainment in water diversions in the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science* 6(2): Article 2. Available at <http://escholarship.org/uc/item/7v92h6fs>

Kimmerer, W.J., E.S. Gross, and M.L. MacWilliams. 2009. Is the response of estuarine nekton to freshwater flow in the San Francisco Estuary explained by variation in habitat volume? *Estuaries and Coasts* 32:375-389.

Kimmerer, W.J. and J.J. Orsi 1996. Changes in the zooplankton of the San Francisco Bay estuary since introduction of the clam *Potamocorbula amurensis*. In *San Francisco Bay: The ecosystem*. In: Hollibaugh, J.T. ed., Pacific Division, American Association for the Advancement of Science, San Francisco, CA: 403-424.

Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. *Oecologia* 52:22-30. Available online at: <http://www.springerlink.com/content/q5030586v6647874/>

Lehman, P.W., S. The, G.L. Boyer, M. Nobriga, E. Bass, and C. Hogle. 2010a. Initial impacts of *Microcystis* on the aquatic food web in the San Francisco Estuary. *Hydrobiologia* 637:229-248.

Lehman P.W., S. Mayr, L. Mecum, and C. Enright. 2010b. The freshwater tidal wetland Liberty Island, CA, was both a source and sink of inorganic and organic material to the San Francisco Estuary. *Aquatic Ecology* 44:359-372.

Lindberg, J.C., and C. Marzuola. 1993. Delta smelt in a newly created, flooded island in the Sacramento-San Joaquin Estuary, Spring 1993. BioSystems Analysis Inc. Prepared for California Department of Water Resources, Sacramento, CA. Available online at: http://www.calwater.ca.gov/Admin_Record/C-044803.pdf

Lott, J. 1998. Feeding habits of juvenile and adult delta smelt from the Sacramento-San Joaquin River Estuary. *Interagency Ecological Program Newsletter* 11: 14-19.

Lucas, L.V., J.E. Cloern, J.K. Thompson, et al. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: Restoration implications. *Ecological Applications* 12: 1528-1547.

Mac Nally, R., J.R. Thompson, W.J. Kimmerer, F. Feyrer, K.B. Newman, A. Sih, W.A. Bennett, L.R. Brown, E. Fleishman, S.D. Culberson, and G. Castillo. 2010. An analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). *Ecological Applications* 20: 1417-1430.

Mager, R.C., S.I. Doroshov, J.P. Van Eenennaam, and R.L. Brown. 2004. Early Life Stages of Delta Smelt. In Feyrer, F., L.R. Brown, R.L. Brown, and J.J. Orsi editors. Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society Symposium 39:169-180.

Maunder, M.N. and R.B. Deriso. 2011. A state-space multistage life cycle model to evaluate population impacts in the presence of density dependence: illustrated with application to delta smelt (*Hyposmesus transpacificus*). Canadian Journal of Fisheries and Aquatic Sciences 68:1285-1306.

McGowan, M.F. 1998. Fishes associated with submerged aquatic vegetation, *Egeria densa*, in the Sacramento-San Joaquin Delta in 1998 as sampled by pop nets. Romberg Tiburon Center, San Francisco State University. Unpublished report prepared for the California Department of Boating and Waterways.

McGowan M.F., and A. Marchi. 1998. Fishes collected in submersed aquatic vegetation, *Egeria densa*, in the Delta. Interagency Ecological Program for the Sacramento-San Joaquin Estuary Newsletter 11(1):9-10.

McIvor, C., L.R. Brown, and Z. Hymanson. 1999. Shallow water habitat workshop summary. IEP Newsletter 12(1), [np].

Meng L., and S.A. Matern. 2001. Native and introduced larval fishes of Suisun Marsh, California: the effects of freshwater flow. Transactions of the American Fisheries Society 130:750-765. Available online at: [http://afsjournals.org/doi/abs/10.1577/15488659\(2001\)130%3C0750:NAILFO%3E2.0.CO%3B2](http://afsjournals.org/doi/abs/10.1577/15488659(2001)130%3C0750:NAILFO%3E2.0.CO%3B2)

Merz, J.M., S. Hamilton, P.S. Bergman, and B. Cavallo. 2011. Spatial perspective for delta smelt: a summary of contemporary survey data. California Fish and Game 97: 164-189.

Miller W.J., B.F. Manly, D.D. Murphy, D. Fullerton, and R.R. Ramey. 2012. An investigation of factors affecting the decline of delta smelt (*Hypomesus transpacificus*) in the Sacramento-San Joaquin Estuary. Reviews in Fisheries Science 20:1-19.

Monaco, M.E., S.B. Weisberg, and T.A. Lowery. 1998. Summer habitat affinities of estuarine fish in U.S. mid-Atlantic coastal systems. Fisheries Management and Ecology 5:161-171. Available online at: <http://www3.interscience.wiley.com/journal/120829574/abstract?CRETRY=1&SRETRY=0>

Moyle, P.B., B. Herbold, D.E. Stevens, and L.W. Miller. 1992. Life history of delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77. Available online at: [http://afsjournals.org/doi/abs/10.1577/15488659\(1992\)121%3C0067:LHASOD%3E2.3.CO%3B2](http://afsjournals.org/doi/abs/10.1577/15488659(1992)121%3C0067:LHASOD%3E2.3.CO%3B2)

Moyle PB. 2002. Inland Fishes of California. University of California Press, Berkeley.
National Research Council. 2011. A review of the use of science and adaptive management in California's Draft Bay-Delta Conservation Plan. National Academies Press. Washington, D.C.

Murphy D.D. and S. A. Hamilton. 2013. Eastward migration or marsh-ward dispersal: understanding seasonal movements by delta smelt. San Francisco Estuary and Watershed Science: in press.

Newman, K.B. 2008. Sample design-based methodology for estimating delta smelt abundance. San Francisco Estuary and Watershed Science 6(3).

Nichols F.H., J.E. Cloern, S.N. Luoma, and D.H. Peterson. 1986. The modification of an estuary. Science 231:567-573. Available online at:
<http://adsabs.harvard.edu/abs/1986Sci...231..567N>

Nobriga, M.L. 1998. Evidence of food limitation in larval delta smelt. Interagency Ecological Program Newsletter 11(1): 20-24.

Nobriga, M.L. 2002. Larval delta smelt composition and feeding incidence: environmental and ontogenetic influences. California Fish and Game 88:149-164.

Nobriga, M.L., F. Feyrer, R. Baxter, and M. Chotkowski. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785. Available online at:
[http://www.iep.ca.gov/AES/Nobriga et al 2005.pdf](http://www.iep.ca.gov/AES/Nobriga_et al 2005.pdf)

Nobriga, M.L., and B. Herbold. 2009. The little fish in California's water supply: a literature review and life-history conceptual model for delta smelt (*Hypomesus transpacificus*) for the Delta Regional Ecosystem Restoration and Implementation Plan (DRERIP). Available online at: http://www.dfg.ca.gov/ERP/conceptual_models.asp

Nobriga, M.L., T.R. Sommer, F. Feyrer, and D. Fleming. 2008. Long-term trends in summertime habitat suitability for delta smelt (*Hypomesus transpacificus*). San Francisco Estuary and Watershed Science 6: Issue 1 (February), Article 1. Available on line at: <http://repositories.cdlib.org/jmie/sfews/vol6/iss1/art1>

Noon, B.R., D.D. Murphy, S.R. Beissinger, M.L. Shaffer, and D. DellaSala. 2003. Conservation planning for US National Forests: conducting comprehensive biodiversity assessments. BioScience 53: 1217-1220.

Norgaard, R.B., G. Kallis, and M. Kiparsky. 2009. Collectively engaging complex socio-ecological systems: Re-envisioning science, governance, and the California delta. Environmental Science and Policy 12: 644-652.

NRC 2011. A review of the use of science and adaptive management in California's draft Bay Delta Conservation Plan. National Academies Press.

Pardue, G.B. 1983. Habitat suitability index models: alewife and blueback herring. U.S. Fish and Wildlife Service FWS/OBS-82/10.58.

Peery, M.Z., S.R. Bessinger, S.H. Newman, B.H. Becker, E. Burkett and T.D. Williams. 2004. Individual and temporal variation in inland flight behavior of marbled murrelets: implications for population monitoring. *Condor* 106:344-353.

Reed, M.J., H.R. Akcakaya, M. Burgman, et al. 2006. Critical Habitat. In: *The Endangered Species Act at thirty*. Scott, J.M., D.D. Goble and F.W. Davis. Island Press, Covelo, CA.

Rosenfield, J.A., and R.D. Baxter. 2007. Population dynamics and distribution patterns of longfin smelt in the San Francisco Estuary. *Transactions American Fisheries Society* 136:1577- 1592. Available online at: <http://afsjournals.org/doi/abs/10.1577/T06-148.1>

Sommer T.R., C. Armor, R.D. Baxter, R. Breuer, L.R. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W.J. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* 32:270-277.

Sommer, T.R., W.R. Harrell, R. Kurth, F. Feyrer, S.C. Zeug, and G. O'Leary. 2004a. Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco Estuary. Pages 111-123 in F. Feyrer, L.R. Brown, R.L. Brown, and J.J. Orsi, editors. *Early Life History of Fishes in the San Francisco Estuary and Watershed*. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Sommer T.R., W.C. Harrell, A. Mueller-Solger, B. Tom, Kimmerer W.J. 2004b. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:247-261. Available online at: <http://www.iep.ca.gov/AES/Aquatic%20Conserv%20Manuscript.pdf>

Sommer, T., F.H. Meija, M.L. Nobriga, F. Feyrer, L. and Grimaldo. 2011. The spawning migration of delta smelt in the upper San Francisco Estuary. *San Francisco Estuary and Watershed Science* 9(2).

Sommer T.R. and F. Meija. 2013. A place to call home: A synthesis of delta smelt habitat in the upper San Francisco estuary. *San Francisco Estuary and Watershed Science*: in press.

Stier, D.J., and J.H. Crance. 1985. Habitat suitability index models and instream flow suitability curves: American shad. U.S. Fish and Wildlife Service Biological Report 82(10.88).

Swanson C., T. Reid, P.S. Young, and J.J. Cech. 2000. Comparative environmental tolerances of threatened delta smelt (*Hypomesus transpacificus*) and introduced wakasagi (*H. nipponensis*) in an altered California estuary. *Oecologia* 123:384-390.

Available online at: <http://www.springerlink.com/content/t1440mrxbhn2cwua/>

Thompson, J. 1957. Settlement geography of the Sacramento-San Joaquin Delta, California. Dissertation, Stanford University.

Thomson, J., et al. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications* 20:1431-1448.

URS. 2007. Status and Trends of Delta-Suisun Services. Report prepared for the California Department of Water Resources, May 2007.

U.S. Fish and Wildlife Service. 1997. Recovery plan for the threatened marbled murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California.

U.S. Fish and Wildlife Service. 2004. Five-year review of the delta smelt. August 1, 2003. *Federal Register* 68(148): 45270-45271.

U.S. Fish and Wildlife Service. 2008. Delta smelt biological opinion on the coordinated operations of the Central Valley Project and State Water Project.

U.S. Fish and Wildlife Service. 2013. Draft revised recovery plan for the Pallid Sturgeon (*Scaphirhynchus albus*).

van Geen, A., and S.N. Luoma. 1999. The impact of human activities on sediments of San Francisco Bay, California: an overview. *Marine Chemistry* 64: 1-6.

Wang JC. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary. Technical Report 9. FS/B10-4ATR 86-9.

Weinstein M.P. 1986. Habitat suitability models: inland silverside. U.S. Fish & Wildlife Service Biological Report 82(10.120).

Whipple, A., R.M. Grossinger, D. Rankin, B. Stanford and R. Askevold. 2012. Sacramento-San Joaquin Delta historical ecology investigation: exploring pattern and process. San Francisco Estuary Institute.

Winder, M. and A.D. Jassby. 2010. Shifts in zooplankton community structure: implications for food web processes in the upper San Francisco Estuary. *Estuaries and Coasts*...

Table 1. *Candidate habitat attributes that may affect the distribution and abundance of delta smelt.*

Aquatic/hydraulic attributes of delta waters

1. Physical water-quality properties (turbidity, salinity, temperature)
2. Chemical water-quality properties (dissolved oxygen, pH)
3. Presence, concentration, absence of contaminants
4. Flow velocity

Biological attributes of the estuary

1. Prey availability (types and densities of food source items)
2. Predation pressure
3. Areal extent, type, and density of aquatic vegetation
4. Presence of *Microcystis*

Physical attributes of the estuary

1. Type of water body
 2. Depth of channel/water body
 3. Width of channel/water body
 4. Extent of proximate shallow water
 5. Substrate structure and composition (grain size, organic content)
 6. Distance to wetlands
-

Table 2. *Delineation of life stages used to examine delta smelt affinity for habitat attributes. Monitoring program data used for each life stage description (either fish length or reproductive stage), and months and years of sampling data used in our study are described. Gonadal stages of male and female delta smelt found in spring Kodiak Trawl database were classified by CA Department of Fish and Game (CDFG) following Mager (1986). Descriptions of reproductive stages are available at <http://www.dfg.ca.gov/delt/data/skt/eggstages.asp>*

	Sub-juveniles	Juveniles	Juveniles	Sub-adults	Mature Adults: Pre-spawning	Mature Adults: spawning
Monitoring Program	20-mm	20-mm	STN	FMWT	Kodiak	Kodiak
Life Stage Distinction	≥ 15, <30mm	30-55 mm	30-55 mm	> 55 mm	Reproductive stages: females 1-3, males 1-4	Reproductive stages: females 4, males 5
Time Period	May-Jun	Jun-Jul	Jun-Aug	Sep-Oct	Jan-Feb	Mar-Apr
Years of data used in this study	1995-2009	1995-2009	1967-2009	1967-2009	2002-2009	2002-2009

Table 3. *Specification of covariates and sources of data for the affinity analyses.*

Attribute	Method of measurement or category list	Source description or derivation
Turbidity	Secchi depth (cm)	IEP ¹ Monitoring Programs
Salinity	Electrical Conductivity (Ec)	IEP ¹ Monitoring Programs
Temperature	Degrees Celsius	IEP ¹ Monitoring Programs
Water body type	Bay-Shoal	Station in a bay overlying a shoal
	Bay Channel	Station in a bay overlying a channel >5 m deep
	River	Station on the Sacramento, San Joaquin or Mokelumne Rivers upstream from their confluence
	Channel	Station on a predominantly anthropogenic, tidally influenced channel
	Slough	
Depth	Average depth within 1 km of station	http://sfbay.wr.usgs.gov/sediment/sfbay/downloads.html http://sfbay.wr.usgs.gov/sediment/delta/downloads.html
Width	Water body width (meters)	GIS (ArcInfo) calculated water body width (meters) based on water boundaries digitized from aerial imagery perpendicular to flow.
Area of shallow water	Area of water less than 2 meters deep within 1 km of station	http://sfbay.wr.usgs.gov/sediment/sfbay/downloads.html http://sfbay.wr.usgs.gov/sediment/delta/downloads.html
Substrate composition (categories)	Rip-rap	>3/4 rip-rap, <1/3 vegetated over
	Cobble-gravel	<3/4 rip-rap, <1/3 vegetated cover, cobble-gravel dominant
		<3/4 rip-rap, <1/3 vegetated cover, sand dominant
		<3/4 rip-rap, <1/3 vegetated cover, mud dominant
		<3/4 rip-rap, <1/3 vegetated cover, organic material dominant
	Mud	>1/3 vegetated cover, algae dominant
	Organic	>1/3 vegetated dominant, rooted vascular dominant
Prey density	Algal	
	Rooted Vascular	
	Density (#/m ³) of juvenile calenoid copepods for the 20mm survey, or adult calenoid copepods for other surveys, at the nearest	IEP Zooplankton Survey

	zooplankton survey station within 5 km of an IEP station	
Distance to wetlands	Distance in meters to tidal estuarine emergent wetlands greater than 100 ha	http://www.fws.gov/wetlands/Data/DataDownload.html http://www.dfg.ca.gov/biogeodata/gis/veg.asp (California Central Valley Wetlands and Riparian GIS, published 1997, processed from 1992-93 data)

¹The Interagency Ecological Program is a long-standing multi-institutional consortium of state and federal water resources and wildlife agencies that carry out research and monitoring on the estuary's environmental resources. (see -- <http://www.water.ca.gov/iep/>)

IEP Monitoring Programs -- 20mm Survey: <ftp://ftp.dfg.ca.gov/Delta%20Smelt/>
<http://www.dfg.ca.gov/delta/projects.asp?ProjectID=20mm>

Summer Townet Survey

<http://www.dfg.ca.gov/delta/projects.asp?ProjectID=TOWNET>

Fall Midwater Trawl

<http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT>

Spring Kodiak Trawl: <ftp://ftp.dfg.ca.gov/Delta%20Smelt/>

<http://www.dfg.ca.gov/delta/projects.asp?ProjectID=SKT>

Zooplankton Study

<http://www.dfg.ca.gov/delta/projects.asp?ProjectID=ZOOPLANKTON>

Table 4. Affinity ranges for delta smelt for seven environmental attributes in the estuary. This table is a summary of the affinity analyses presented in Appendix A. A “suitable” range depicts conditions where delta smelt demonstrated relative use of an attribute range that is significantly greater than the relative availability of that range. A “weak affinity” range depicts attribute ranges where relative use exceeds relative availability. An “inadequate” range depicts conditions where relative use is significantly less than relative availability.

Affinity		Spring	Spring	Summer	Fall	Winter	Winter
Life-stage		Sub-juvenile	Juveniles	Juveniles	Sub-Adults	Pre-spawning Adults	Spawning Adults
Primary Months		May-Jun	Jun-Jul	Jun-Aug	Sep-Dec	Jan-Feb	Mar-Apr
Program		20mm	20mm	STN	FMWT	Kodiak	Kodiak
Turbidity (Secchi depth cm)	Suitable	20-40	20-40	20-40	30-60	20-30	20-30
	Weak affinity	10-50	10-40	0-50	0-60	0-40	20-50
	Inadequate	>50	>50	>50	60-70,>80	>60	50-60,>70
Salinity (Ec)	Suitable	200-1000	1000-4000	1000-4000	1000-8000	1000-4000	-
	Weak affinity	200-4000	200-8000	1000-8000	200-12000	1000-8000	200-600 1000-8000
	Inadequate	>4000	<200, >16000	<400, >16000	<200, >20000	<200, >8000	<200, >8000
Temperature (Celsius)	Suitable	20-21	20-21	18-22	-	-	-
	Weak affinity	18-22	18-21	18-22	16-21	13-15	12-15
	Inadequate	12-18,>22	16-18,>22	>22	-	-	-
Calenoid Copepods (#/m ³)	Suitable	1000-2500	250-2500	-	>1000	250-1000	-
	Weak affinity	-	100-2500	1000-2500	>250	100-2500	250-1000
	Inadequate	-	<1,>2500	<10	-	-	10-100
Depth (meters)	Suitable	>7	7-9	<3, 7-9	7-9	5-6	5-6
	Weak affinity	various	<3	<3,7-9	6-12	4-6	5-6,>9
	Inadequate	2-4	4-7	4-7	<5	<4,6-7	<4,6-7
Area of Shallows (ha)	Suitable	5-20	>100	>100	5-20	5-20	-
	Weak affinity	5-20, >200	>100	5-20,>100	5-20	5-20,>200	5-20,>200
	Inadequate	20-50	<5	<5,20-100	<5,>20	20-100	50-100
Distance from Wetlands km	Suitable	1-2, 3-5	1-2, 3-5	1-2, 3-5	0.5-2	0-0.25	-
	Weak affinity	1-2, 3-5	0.25-0.5, 1-2, 3-5	0.25-0.5, 1-2, 3-5	0-2	0-0.25,1-2	< 0-0.25, 1-2
	Inadequate	>5	>5	>5	>3	>5	>5

Table 5. Results of multiple regression analysis when distribution of delta smelt (dependent variable) is regressed against the habitat suitability index values of six habitat attributes during various life stages; “negative” indicates the regression coefficient had a negative sign.

Attribute	Sub-juvenile	Juvenile (20mm)	Juvenile (STN)	Sub-adult	Pre-spawning adult	Spawning adult
n	2592	2016	2809	9246	686	614
	Coeff P-value	Coeff P-value	Coeff P-value	Coeff P-value	Coeff P-value	Coeff P-value
Turbidity	0.31 <0.001	0.09 <0.001	0.05 <0.001	0.21 <0.001	0.26 <0.001	0.19 0.001
Salinity	0.17 <0.001	0.22 <0.001	0.47 <0.001	0.37 <0.001	0.81 <0.001	0.29 0.011
Temperature	0.23 <0.001	0.14 <0.001	0.05 0.031	Negative	Negative	0.12 0.774
Depth	0.44 <0.001	0.19 <0.001	0.40 <0.001	0.33 <0.001	0.15 0.041	0.12 0.024
Shallows Area	Negative	Negative	0.18 <0.001	Negative	0.54 <0.001	0.27 0.021
Wetlands Distance	0.02 0.460	0.16 <0.001	0.22 <0.001	0.36 <0.001	0.10 0.139	Negative

Table 6. Results of multiple regression analysis when distribution of delta smelt (dependent variable) is regressed against the habitat suitability index values of seven habitat attributes during various life stages; “negative” indicates that the regression coefficient had a negative sign.

Attribute	Sub-juvenile		Juvenile (20mm)		Juvenile (STN)		Sub-adult		Pre-spawning adult		Spawning adult	
n	2378		1835		2750		5792		424		376	
	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value	Coeff	P-value
Turbidity	0.30	<0.001	0.10	<0.001	0.05	<0.001	0.27	<0.001	0.28	<0.001	0.18	0.012
Salinity	0.19	<0.001	0.20	<0.001	0.44	<0.001	0.40	<0.001	0.53	0.014	0.27	0.141
Temperature	0.25	<0.001	0.15	<0.001	0.06	0.016	0.04	<0.001	0.06	0.694	0.33	0.525
Depth	0.53	<0.001	0.20	<0.001	0.39	<0.001	0.43	<0.001	0.19	0.067	0.11	0.156
Shallows Area	Negative		Negative		0.16	<0.001	Negative		0.82	<0.001	0.21	0.162
Wetlands Distance	0.12	0.009	0.17	<0.001	0.23	<0.001	0.14	<0.001	Negative		Negative	
Prey Density	Negative		0.26	<0.001	0.02	0.061	Negative		0.89	0.002	0.09	0.145

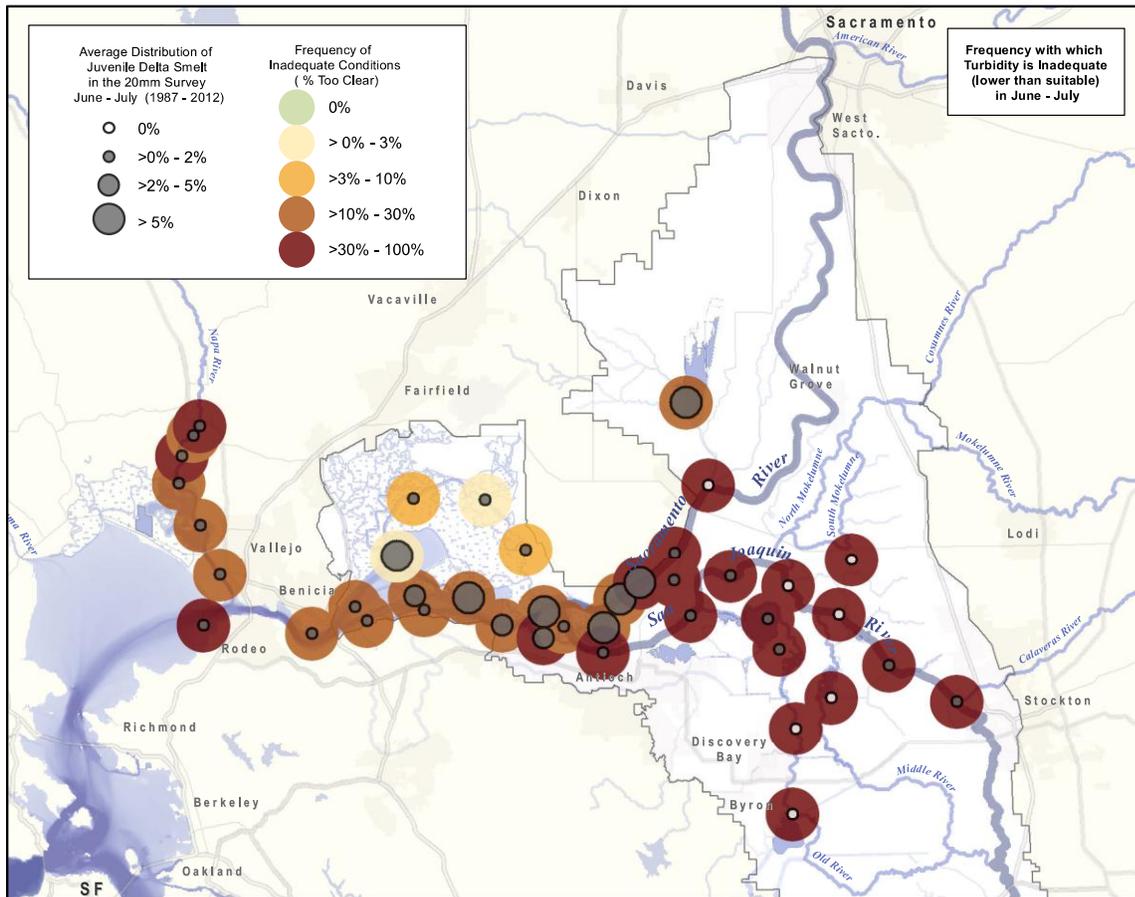


Figure 2. The distribution of juvenile delta smelt from 20mm trawl surveys and the frequency with which turbidity is inadequate (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

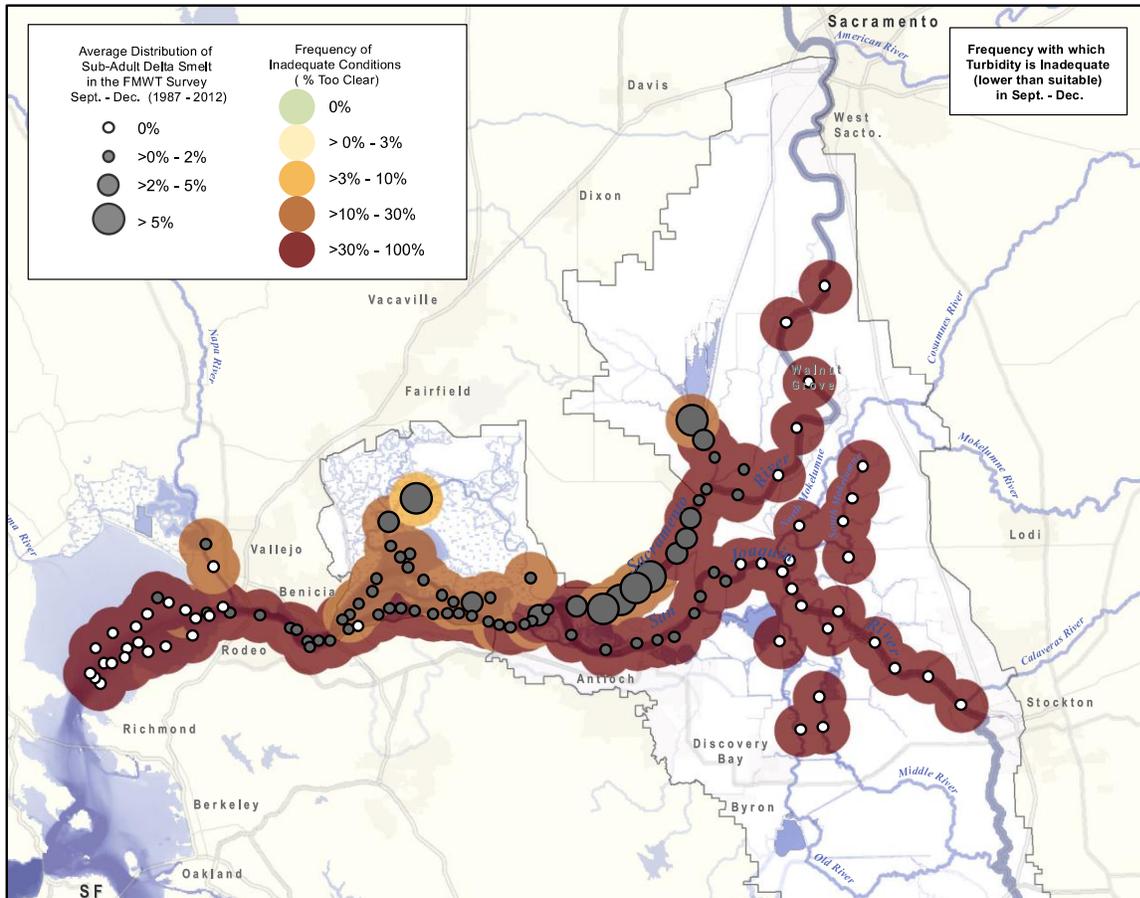


Figure 3. Distribution of sub-adult delta smelt from the Fall Midwater Trawl surveys and the frequency with which turbidity is inadequate (see Table 4). Gray circles indicate the average, across years, of the percentage effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

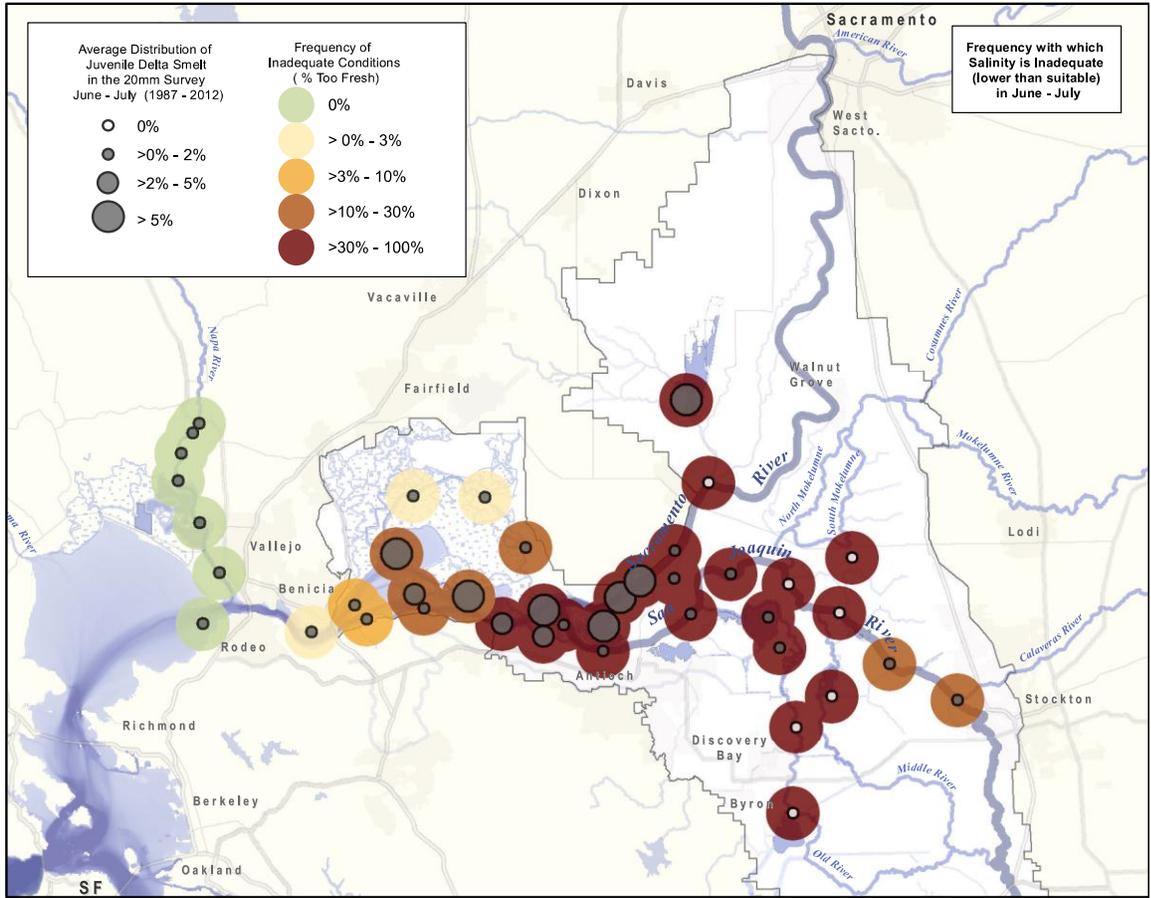


Figure 4. The distribution of delta smelt from 20mm trawl surveys and the frequency with which salinity conditions are inadequate, with salinity levels too low (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

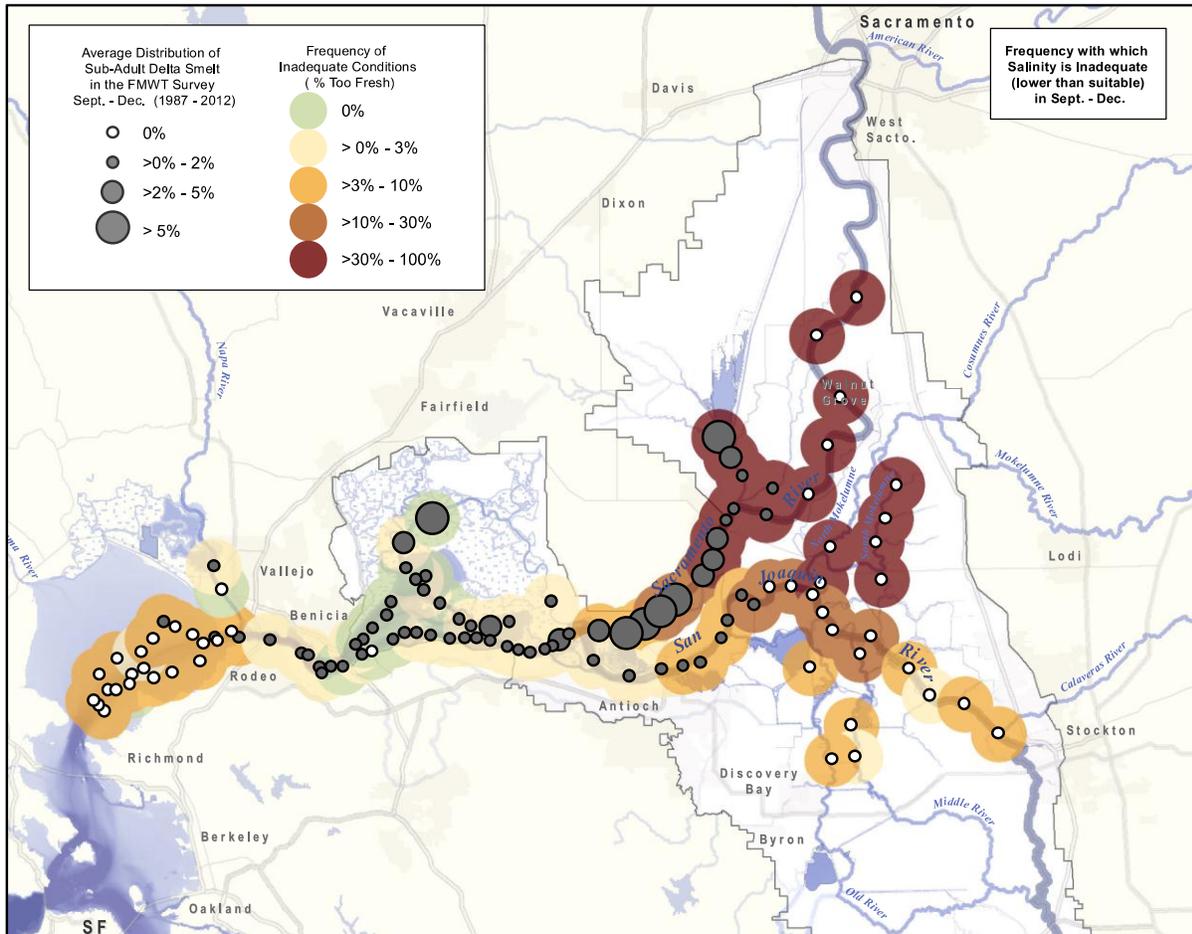


Figure 5. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency with which salinity is inadequate, with salinity levels too low (see Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

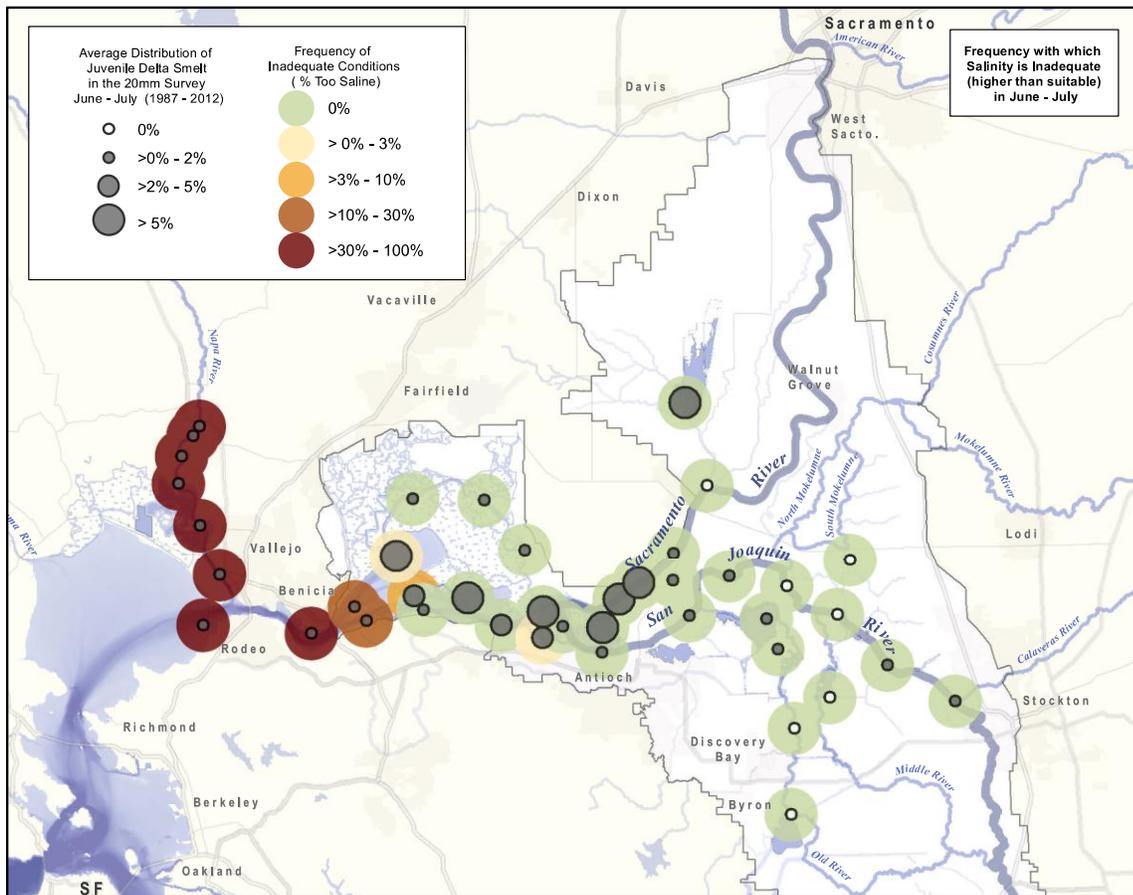


Figure 6. The distribution of delta smelt from the 20mm trawl surveys and the frequency with which salinity is inadequate, with salinity too high (see Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm survey during June and July at each monitoring station.

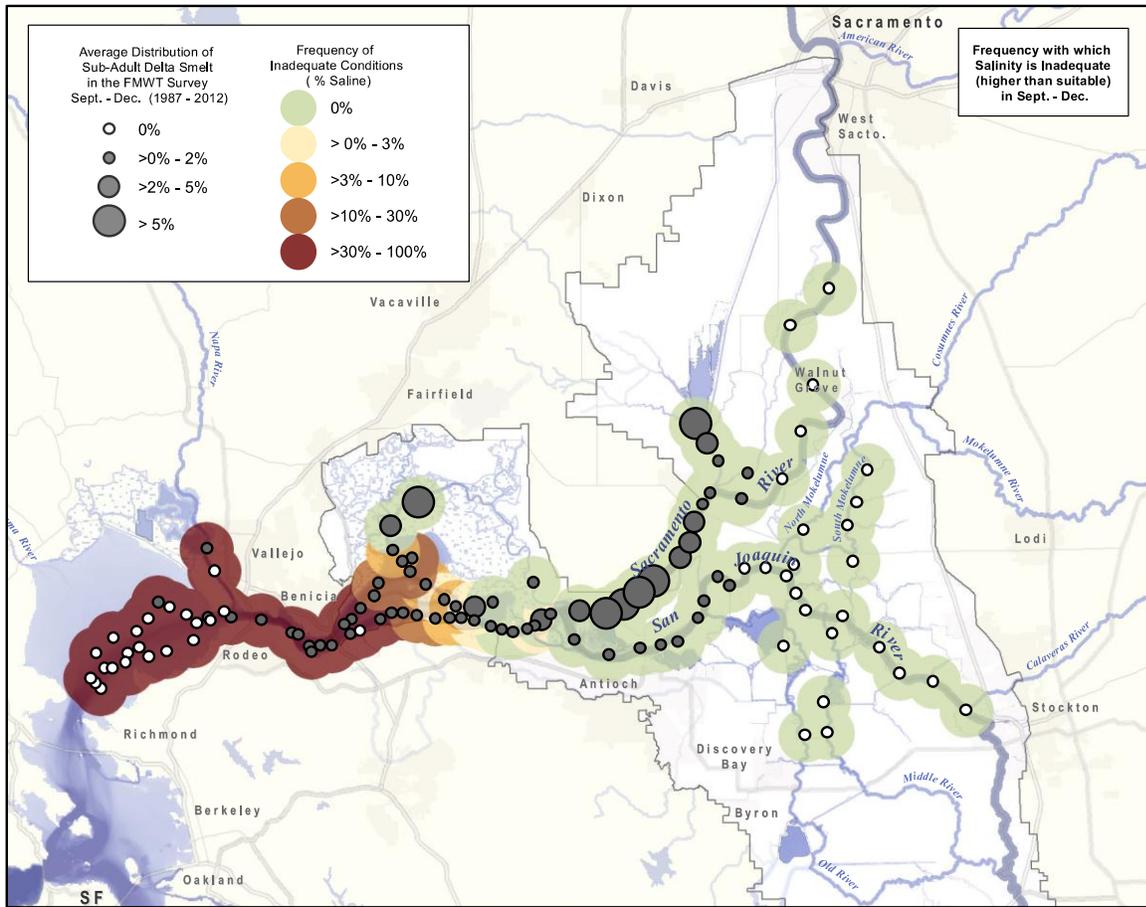


Figure 7. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency in which salinity is inadequate, with salinity too high (Table 4). Gray circles indicate the across-years average of the percentage effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

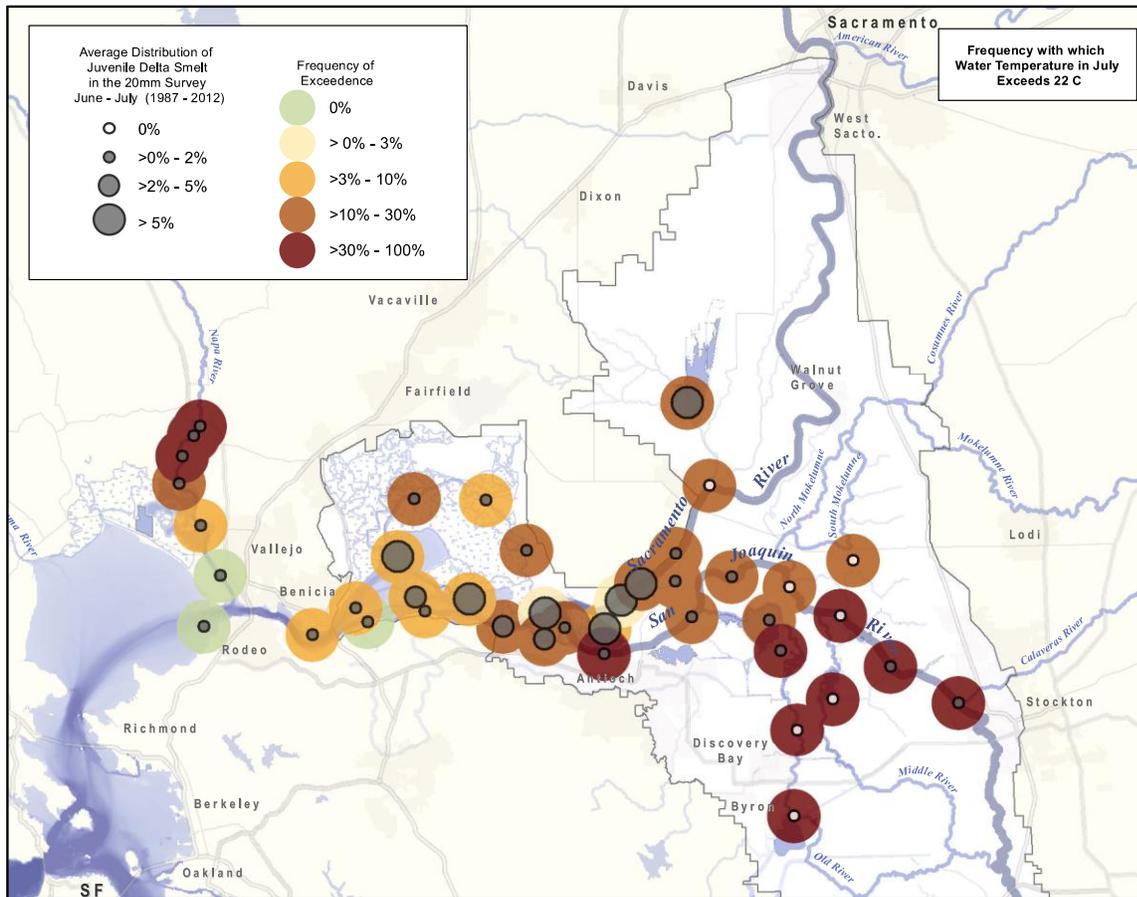


Figure 8. The distribution of delta smelt from the 20mm trawl survey and the frequency with which water temperature in July exceeds the 22-degree C threshold. Gray circles indicate the across-years average of the percentage effort-corrected catch of juvenile delta smelt in the 20 mm survey during June and July at each monitoring station.

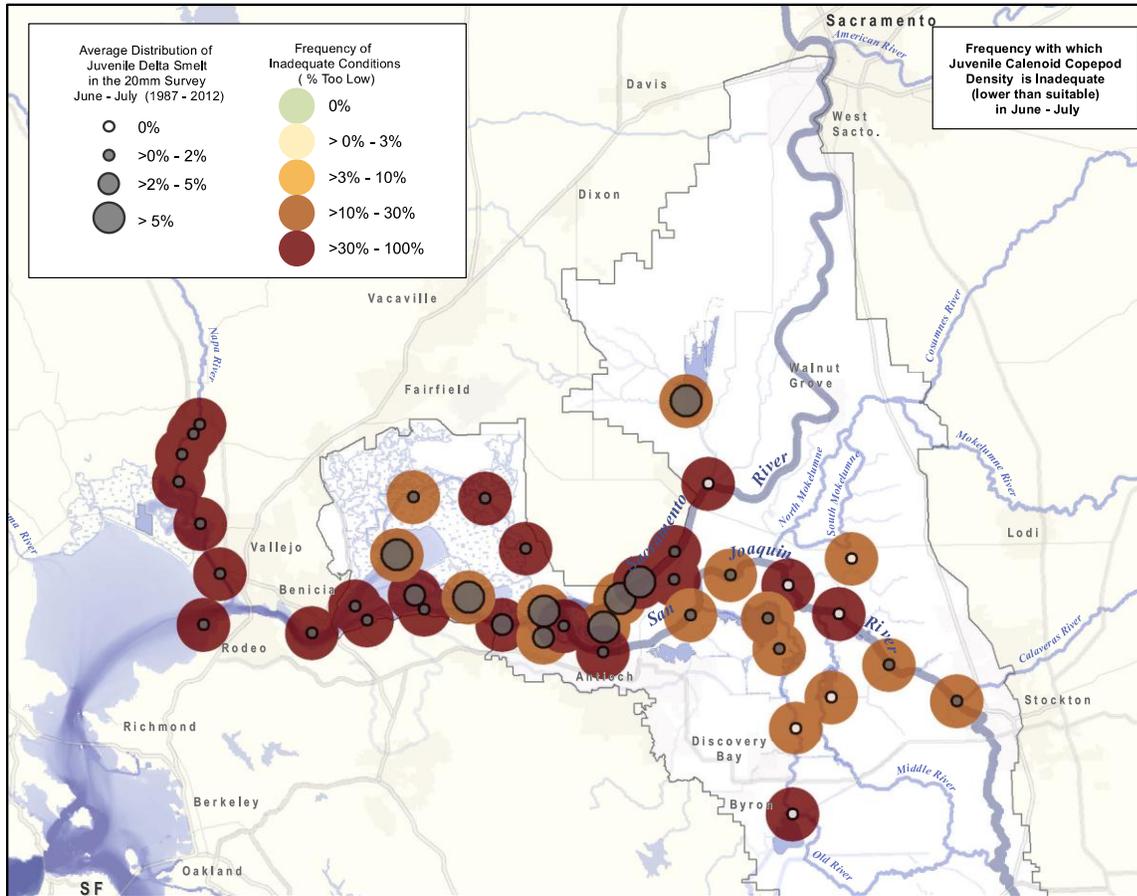


Figure 9. The distribution of delta smelt from the 20mm trawl survey and the frequency with which density of juvenile calanoid copepods is inadequate (Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of juvenile delta smelt in the 20 mm Survey during June and July at each monitoring station.

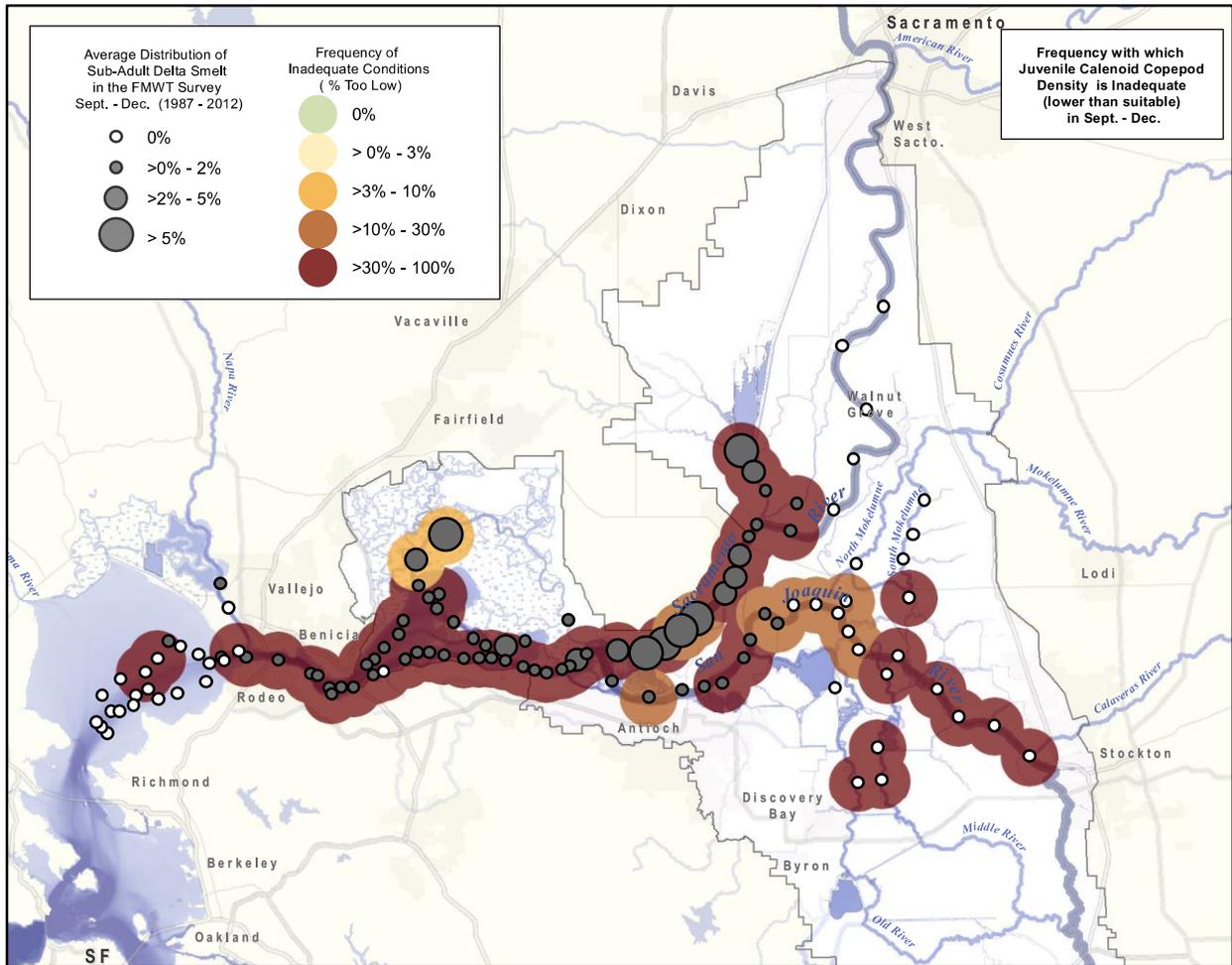


Figure 10. The distribution of delta smelt from the Fall Midwater Trawl survey and the frequency with which density of adult calanoid copepods is inadequate (see Table 4). Gray circles indicate the across-years average of the percentage of the effort-corrected catch of sub-adult delta smelt in the Fall Midwater Trawl Survey from September through December at each monitoring station.

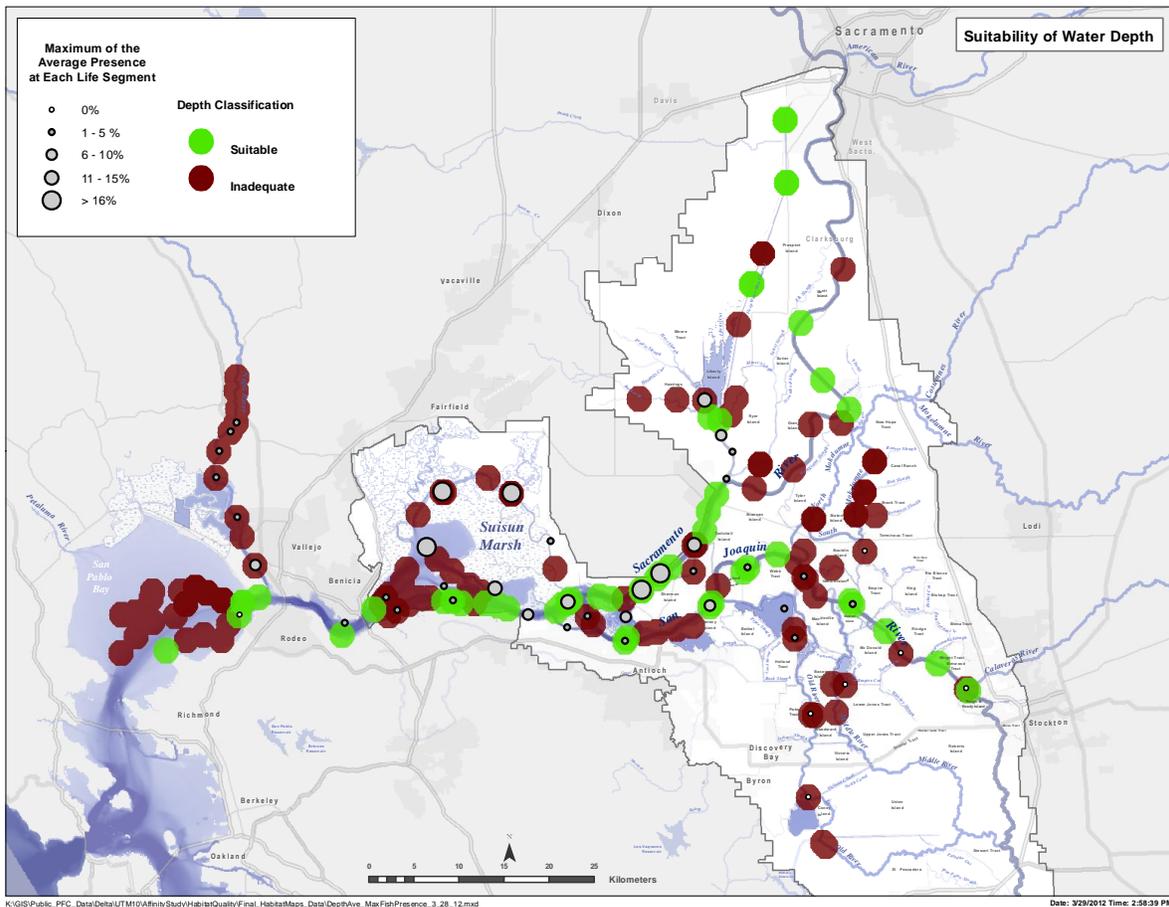


Figure 11. The maximum average presence of each of several life stages of delta smelt (from multiple trawl surveys) and the suitability of proximate water depth. Gray circles indicate the across-years average of the maximum percentage of the effort-corrected catch of delta smelt in any survey at each monitoring station. The colored circles indicate the suitability of average water depth at each station as classified in Table 4.

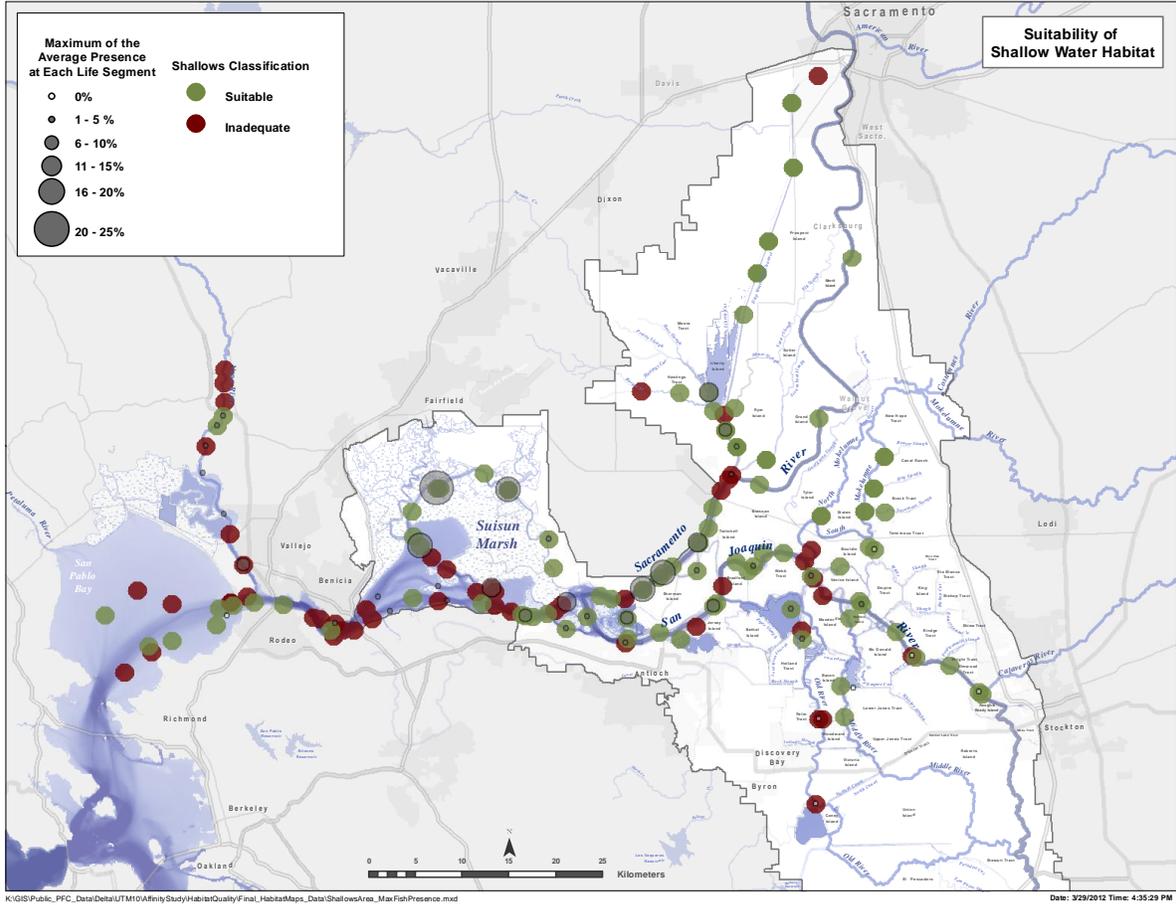


Figure 12. Distribution of the maximum average presence of each life stage of delta smelt, and categorical classification of the availability of shallow water circumstances at and adjacent to survey stations. Gray circles indicate the average, across years, of the maximum percentage effort-corrected catch of delta smelt in any IEP survey at each monitoring station. The colored circles indicate the suitability of the area of shallow water in the vicinity of each station as classified in Table 4.

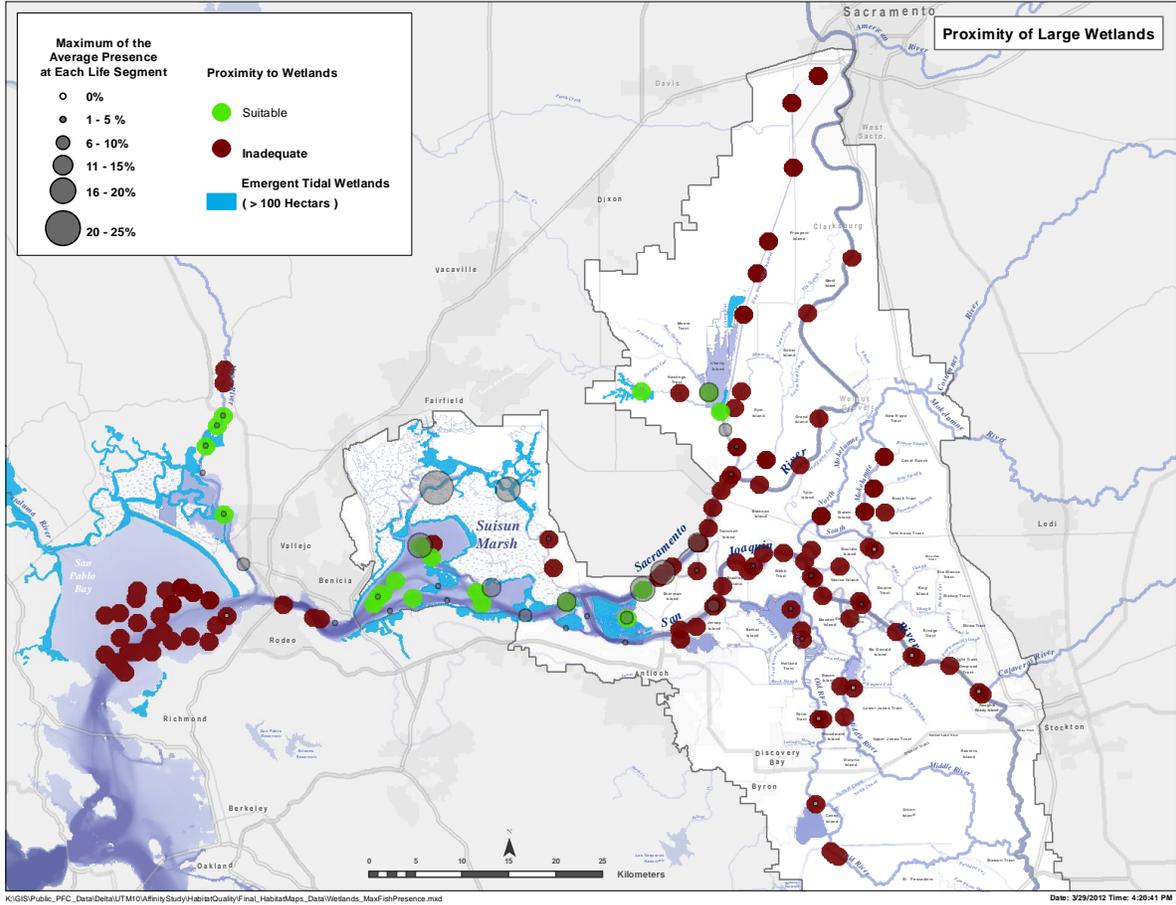


Figure 13. Maximum average presence of multiple delta smelt life stages at trawl survey stations in relation to station distance from wetlands greater than 100 hectares in extent. Gray circles indicate the across-years average of the maximum percentage effort-corrected catch of delta smelt in any IEP survey at each monitoring station. The colored circles indicate the suitability of the proximity of wetlands to each station as classified in Table 4.

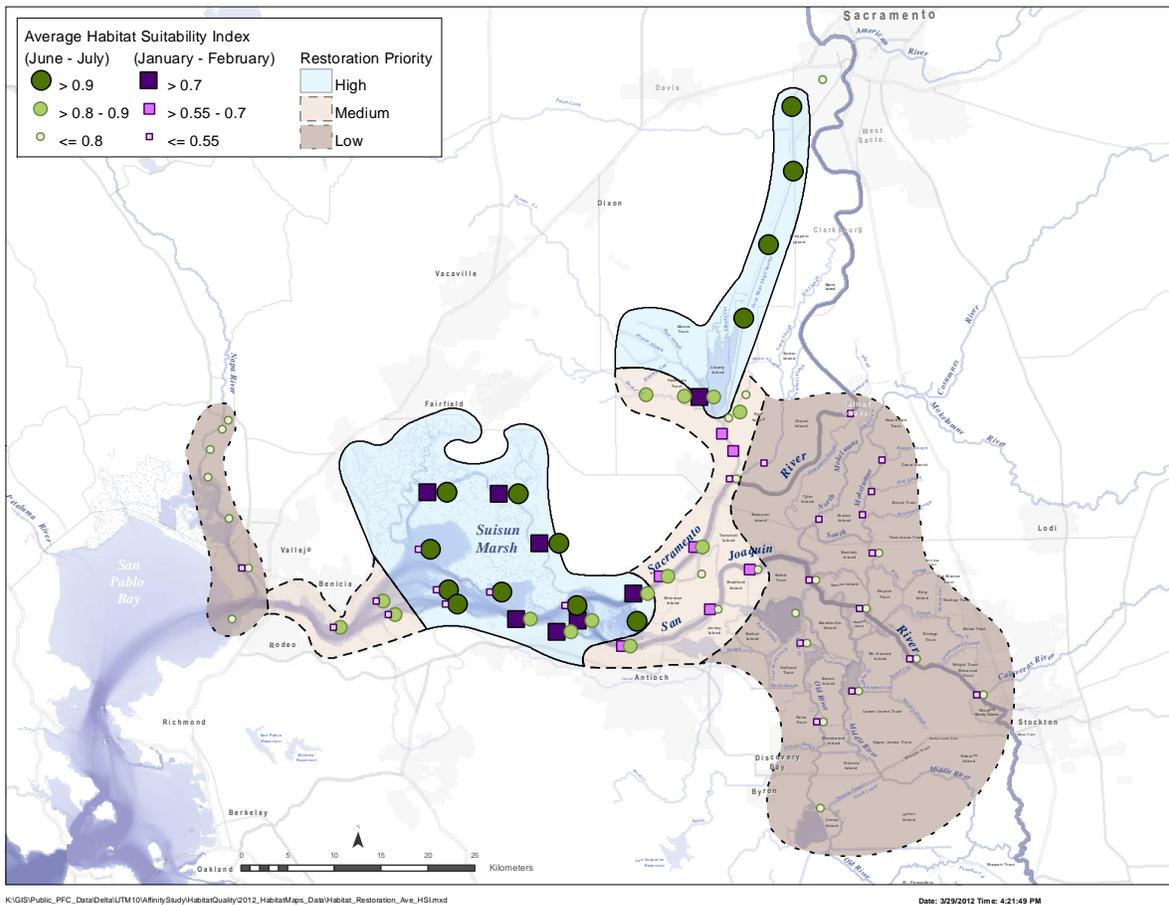
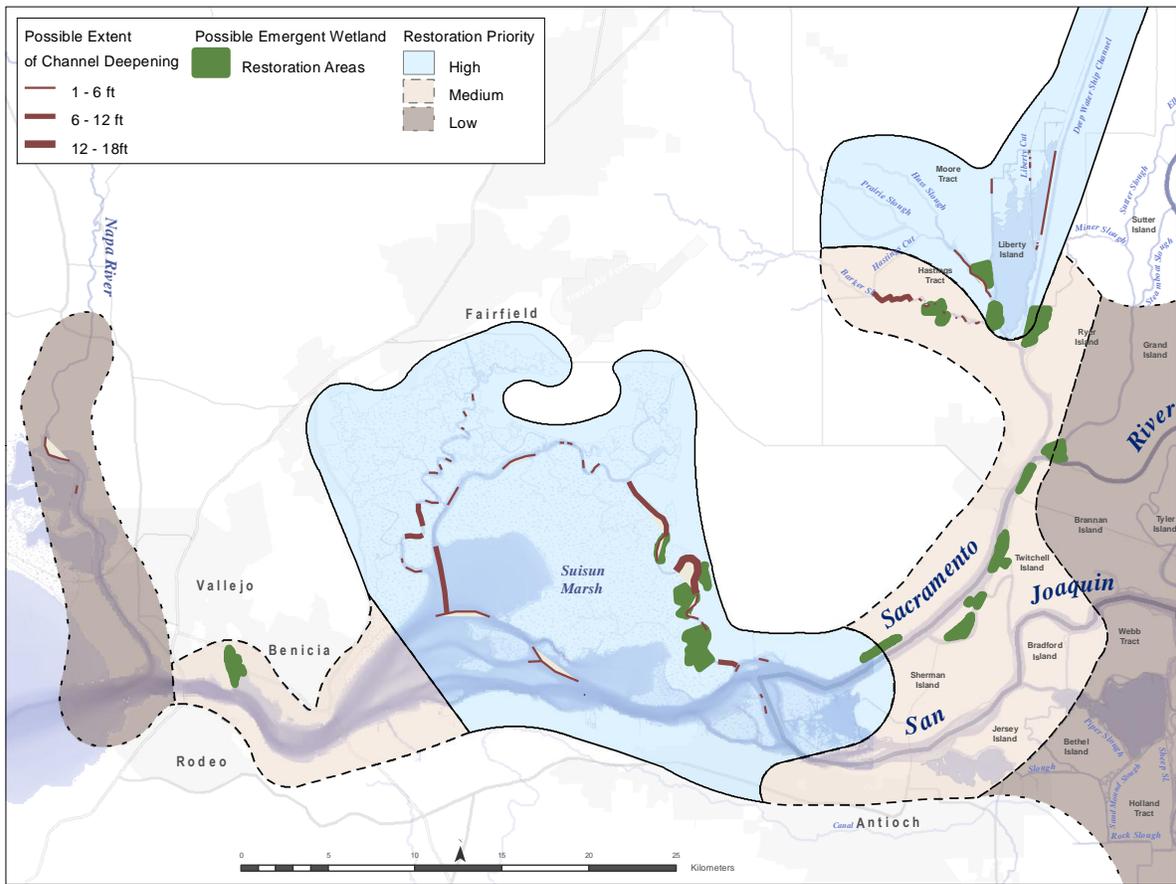


Figure 14. Aggregated suitability for turbidity, salinity, and temperature at Spring Kodiak Monitoring Stations averaged for January and February and 20 mm Monitoring Stations averaged for June and July. The larger, darker symbols represent those stations with higher average weighted habitat suitability index values derived from these three attributes. Areas designated as high priority for restoration (light blue) contain stations with habitat suitability index values in the upper quartile in either survey. Areas designated as medium priority for restoration (tan) contain stations in the second highest quartile in either survey. Areas designated as low priority (grey) contain stations with habitat suitability index values below the median in both surveys.



K:\GIS\Public_PFC_Data\Delta\UTM10\A\InfinyStudy\HabitatQuality\2012_HabitaMaps_Data\Habitat_Restoration_Channel_Wetlands2.mxd

Date: 3/30/2012 Time: 8:55:46 AM

Figure 15. Candidate areas for channel modification and restoration of tidal emergent wetlands. The locations include sites for which environmental variables other than proximity to wetlands are frequently within suitable ranges. Red-tone channel reaches (and other watercourses) are target areas for channel-deepening efforts designed to make local conditions for delta smelt suitable as habitat. The locations for wetlands restoration are sites for which other environmental variables are frequently within suitable ranges, within the current range of delta smelt, close to sea level, and are close to deep-water channel circumstances.

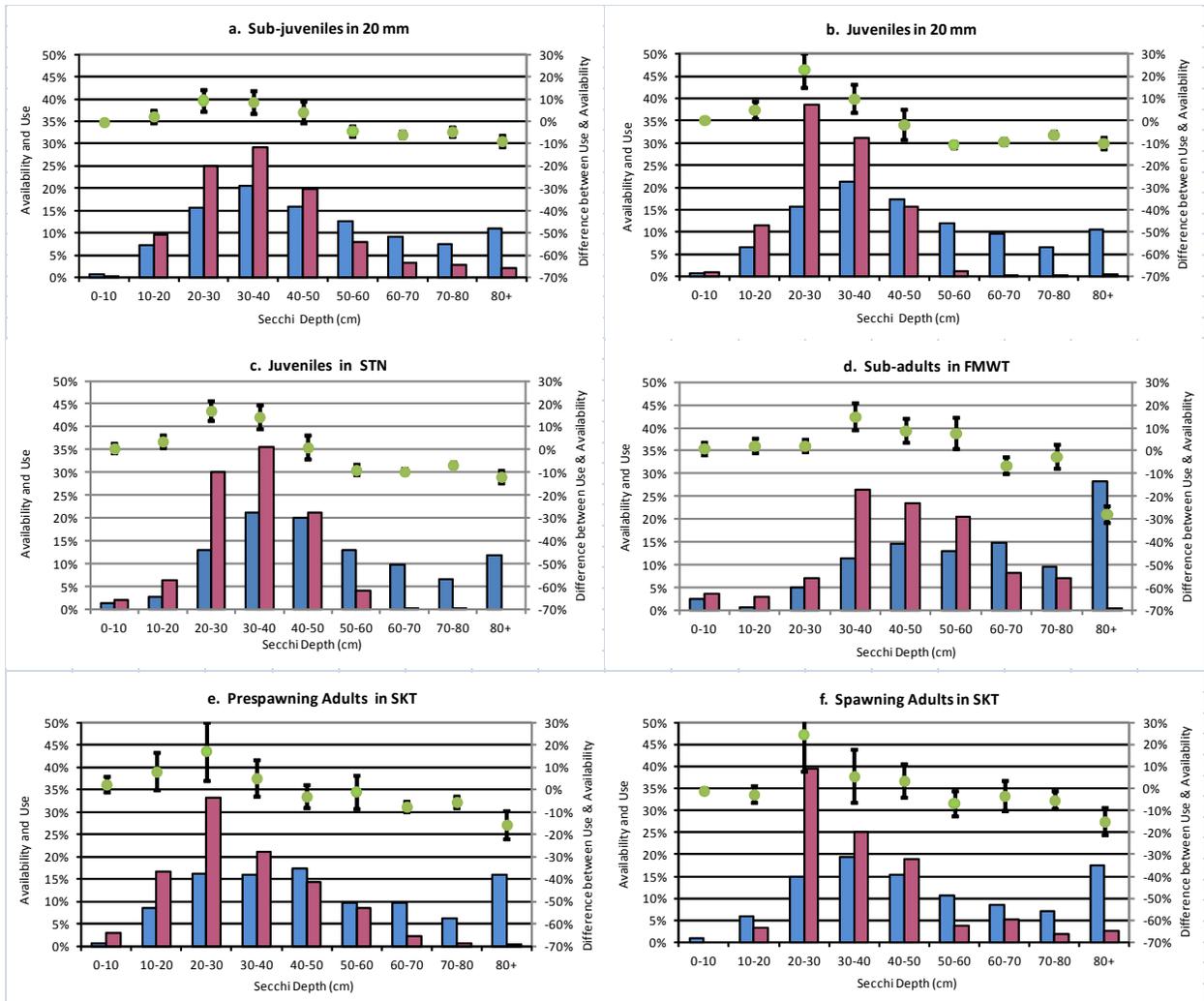


Figure S1. Affinity analysis for water clarity (secchi depth in cm) by life stage. Graphs depict the relative availability of a secchi depth segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

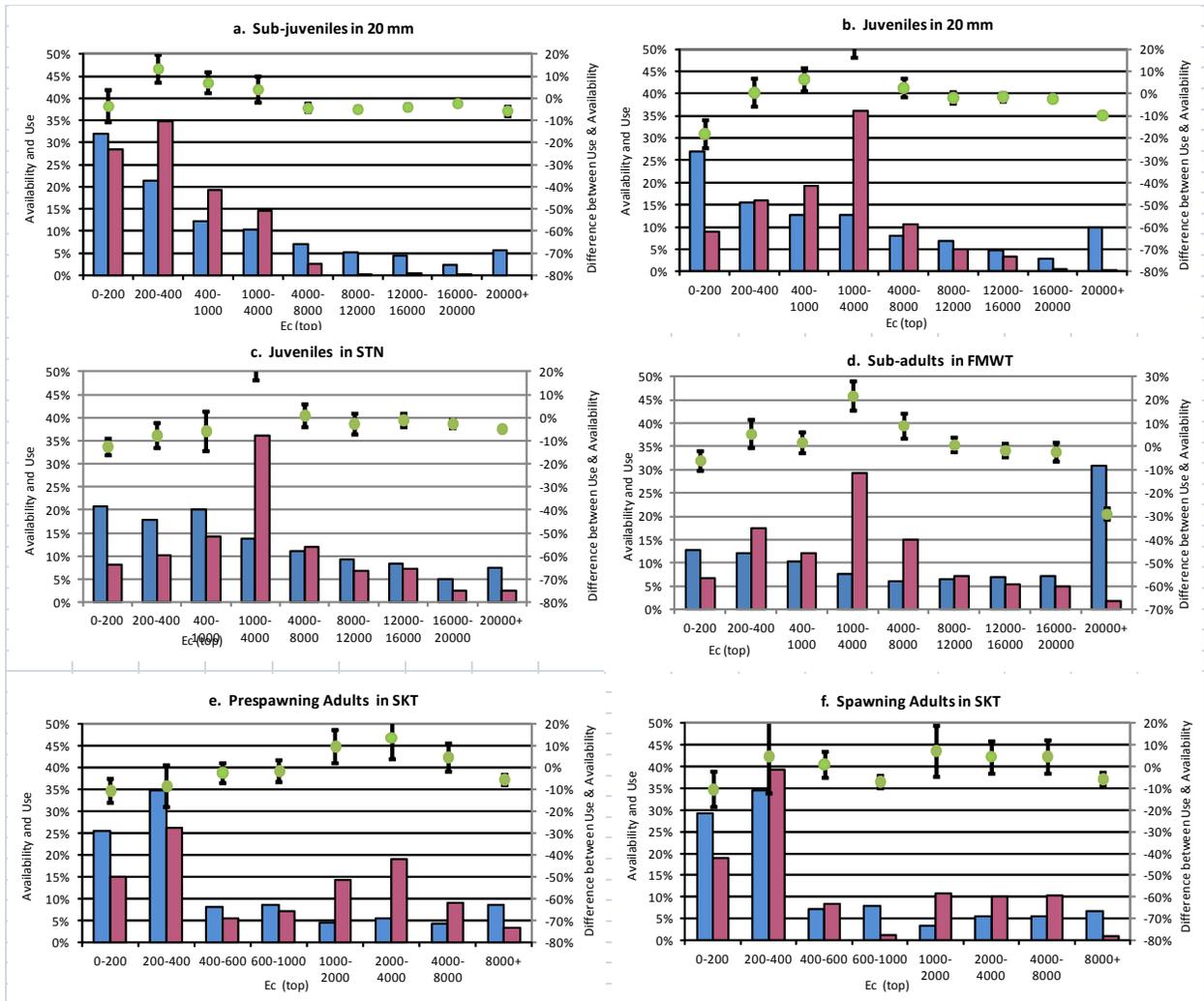


Figure S2. Affinity analysis for salinity (Ec) by life stage. Graphs depict the relative availability of a salinity segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

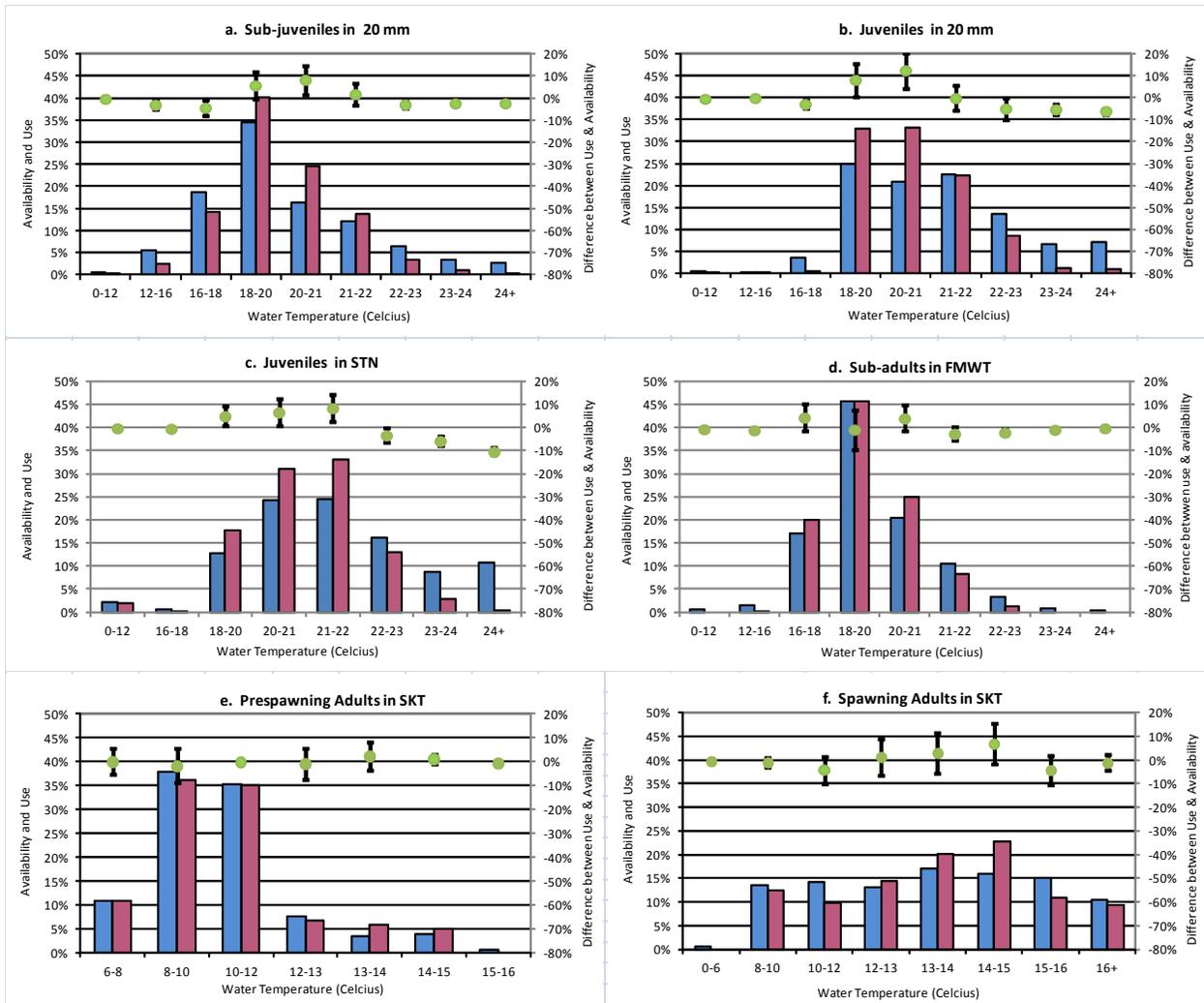


Figure S3. Affinity analysis for water temperature (Celsius) by life stage. Graphs depict the relative availability of a temperature segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

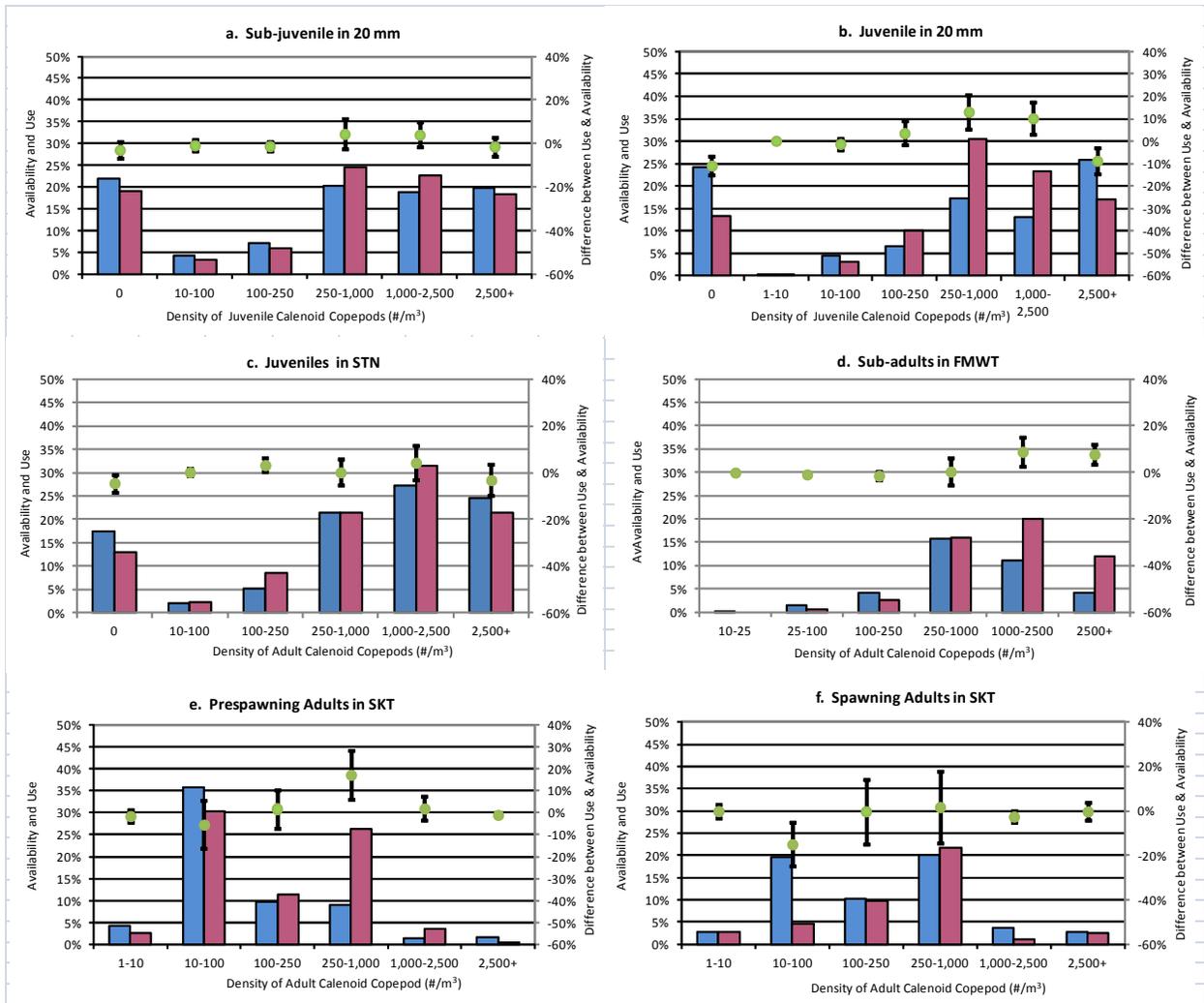


Figure S4. Affinity analysis for density of calenoid copepods by life stage. Graphs depict the relative availability of a calenoid copepod segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

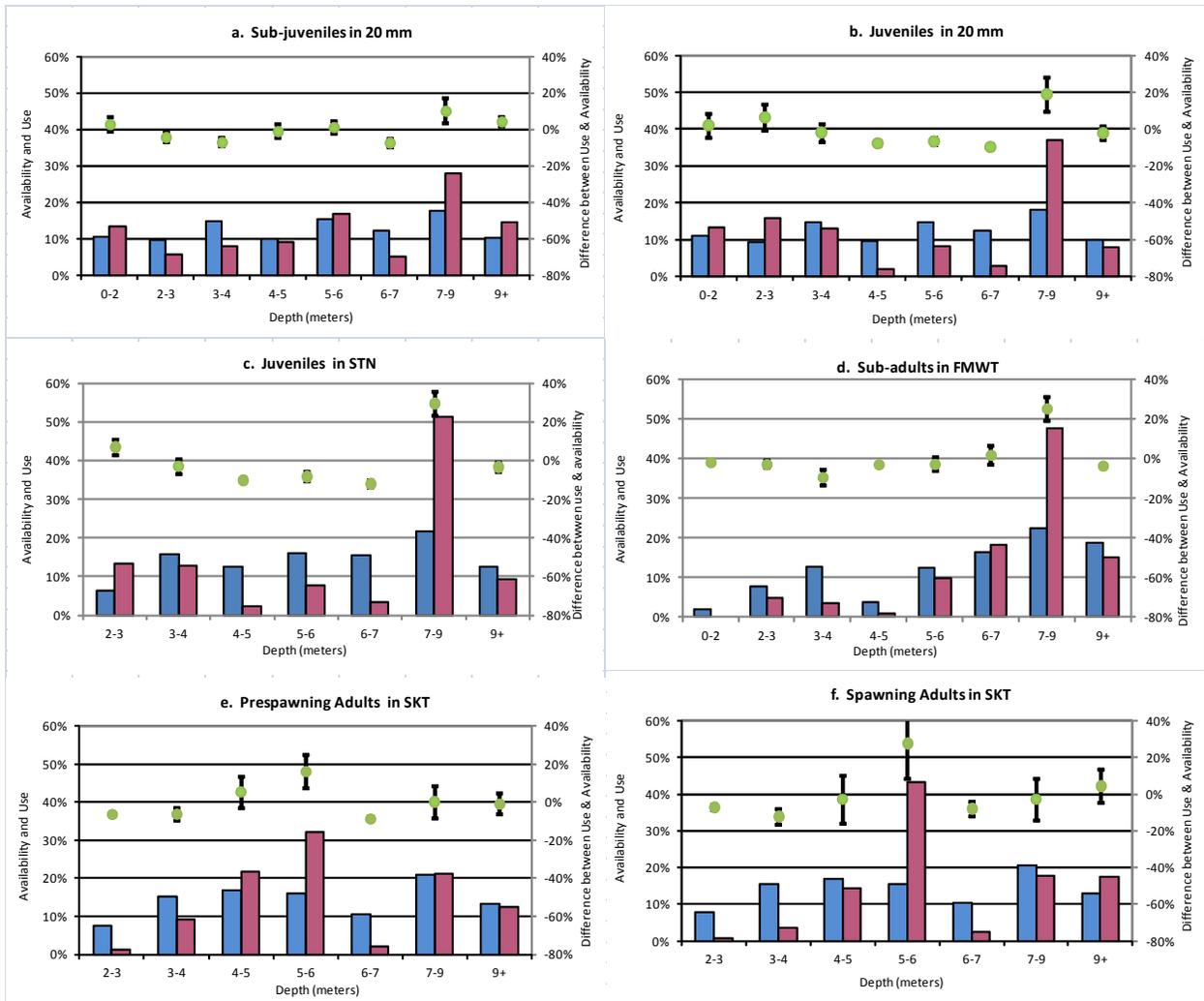


Figure S5. Affinity analysis for water depth (feet) by life stage. Graphs depict the relative availability of a depth segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

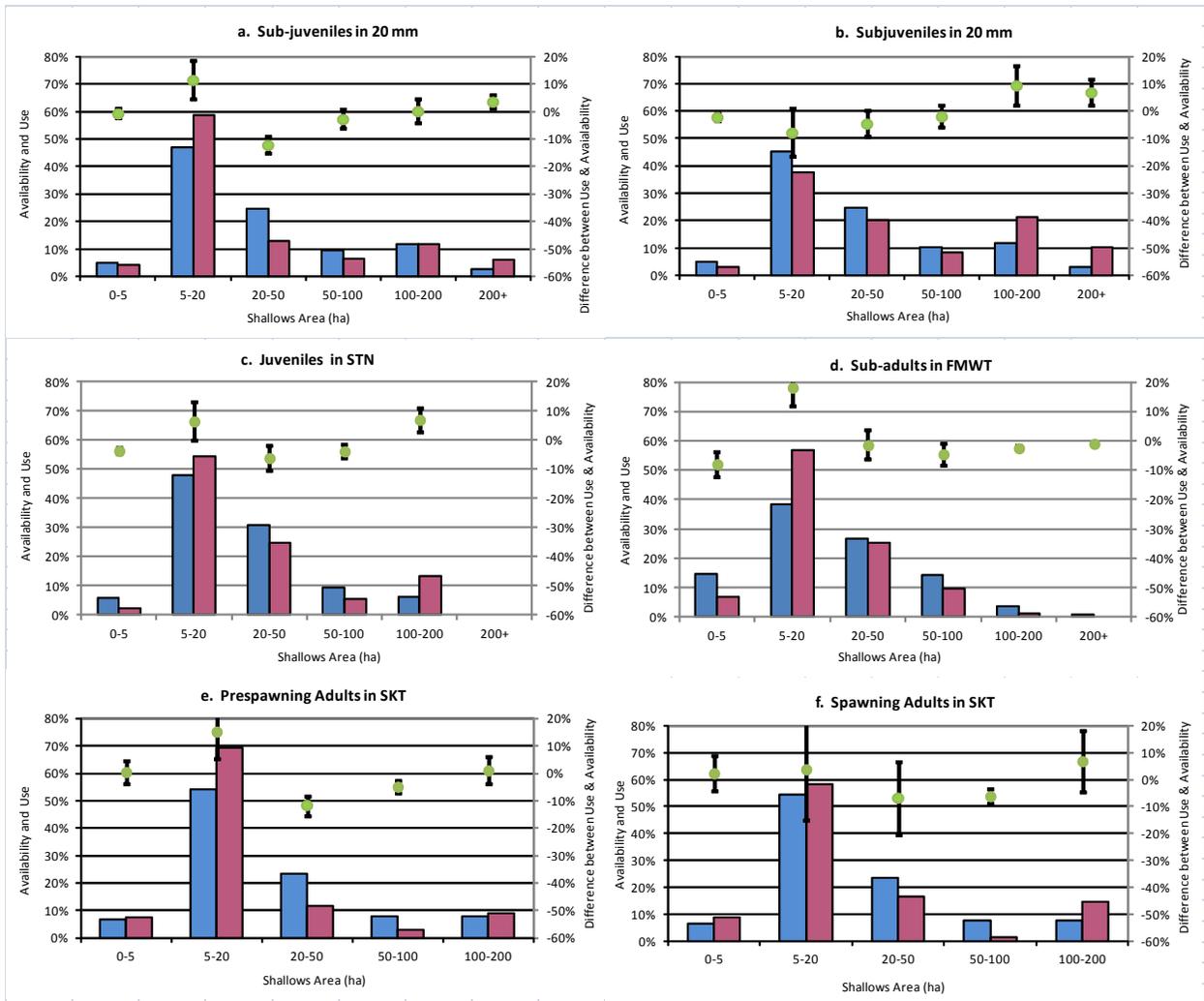


Figure S6. Affinity analysis for area of shallows (water less than 2 meters deep) by life stage. Graphs depict the relative availability of an area-of-shallows segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

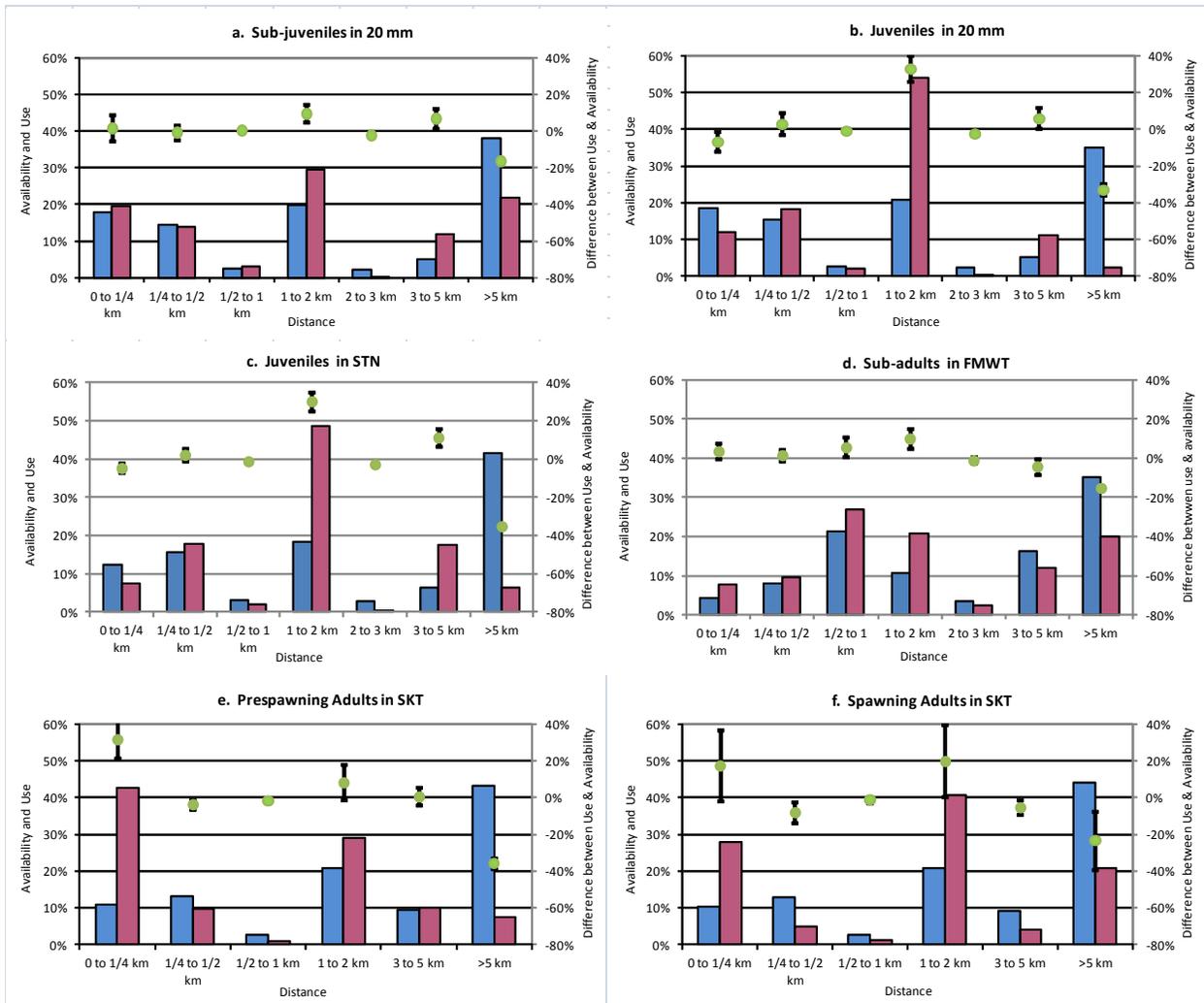


Figure S7. Affinity analysis for distance to large wetlands (wetlands >100ha) by life stage. Graphs depict the relative availability of a distance-to-wetlands segment (blue columns) and the relative use of that segment (red columns). Green dots show the difference between the two columns. The error bars around the green dots show the 90% confidence interval.

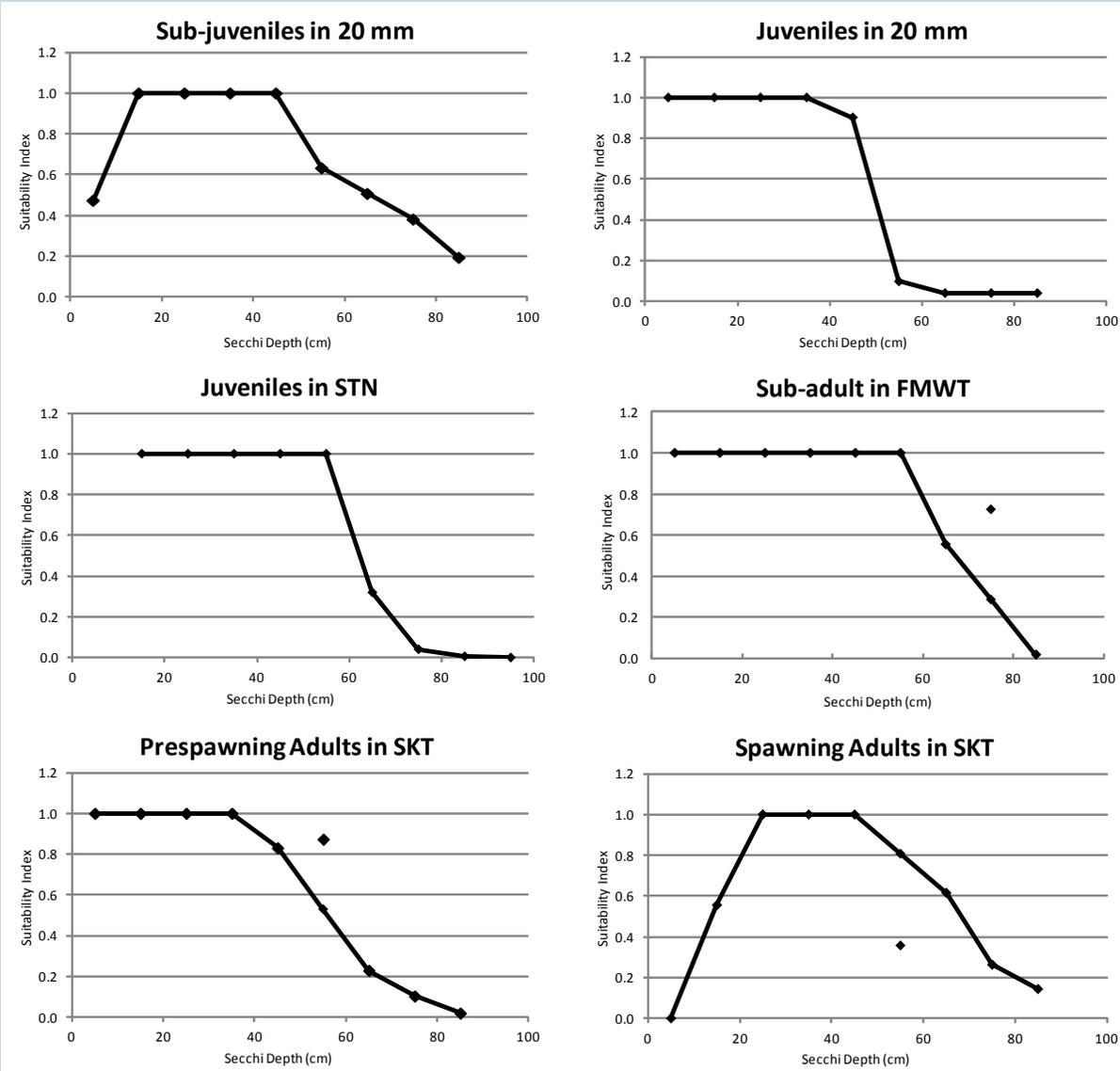


Figure S8. Habitat suitability Index curves for turbidity for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range-segments with a small number of data points.

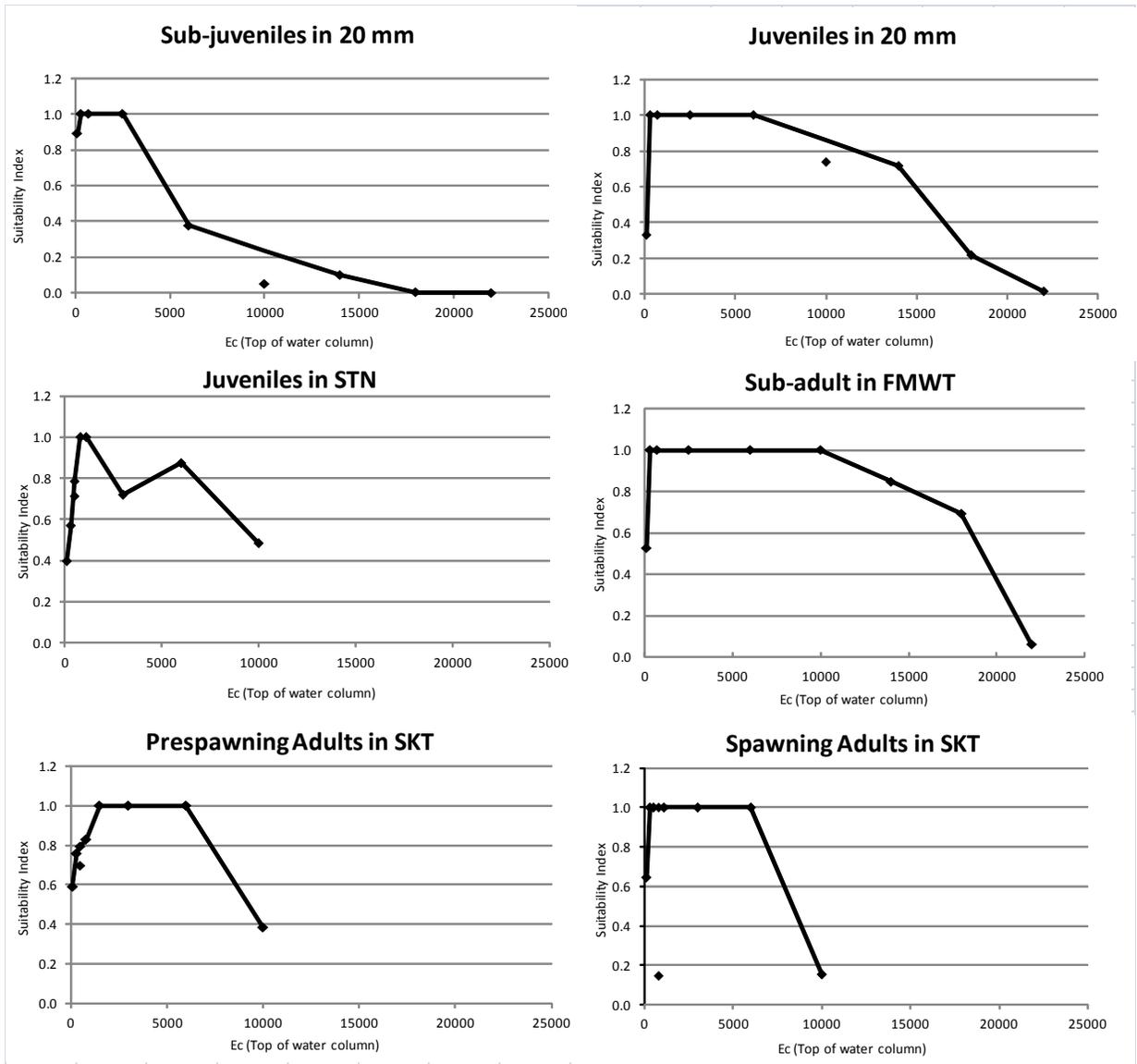


Figure S9. Habitat suitability Index curves for salinity for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

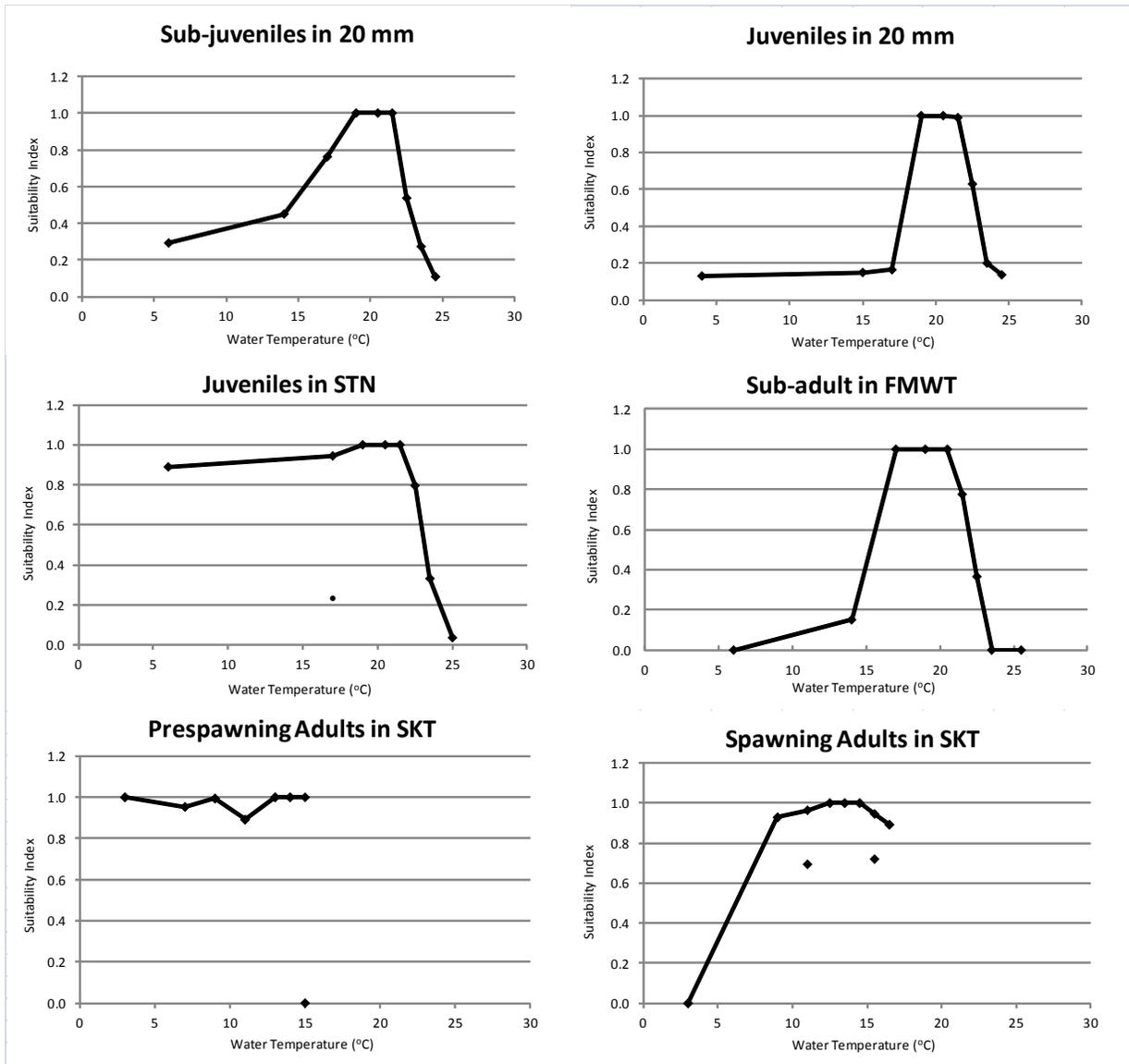


Figure S10. Habitat suitability Index curves for water temperature for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

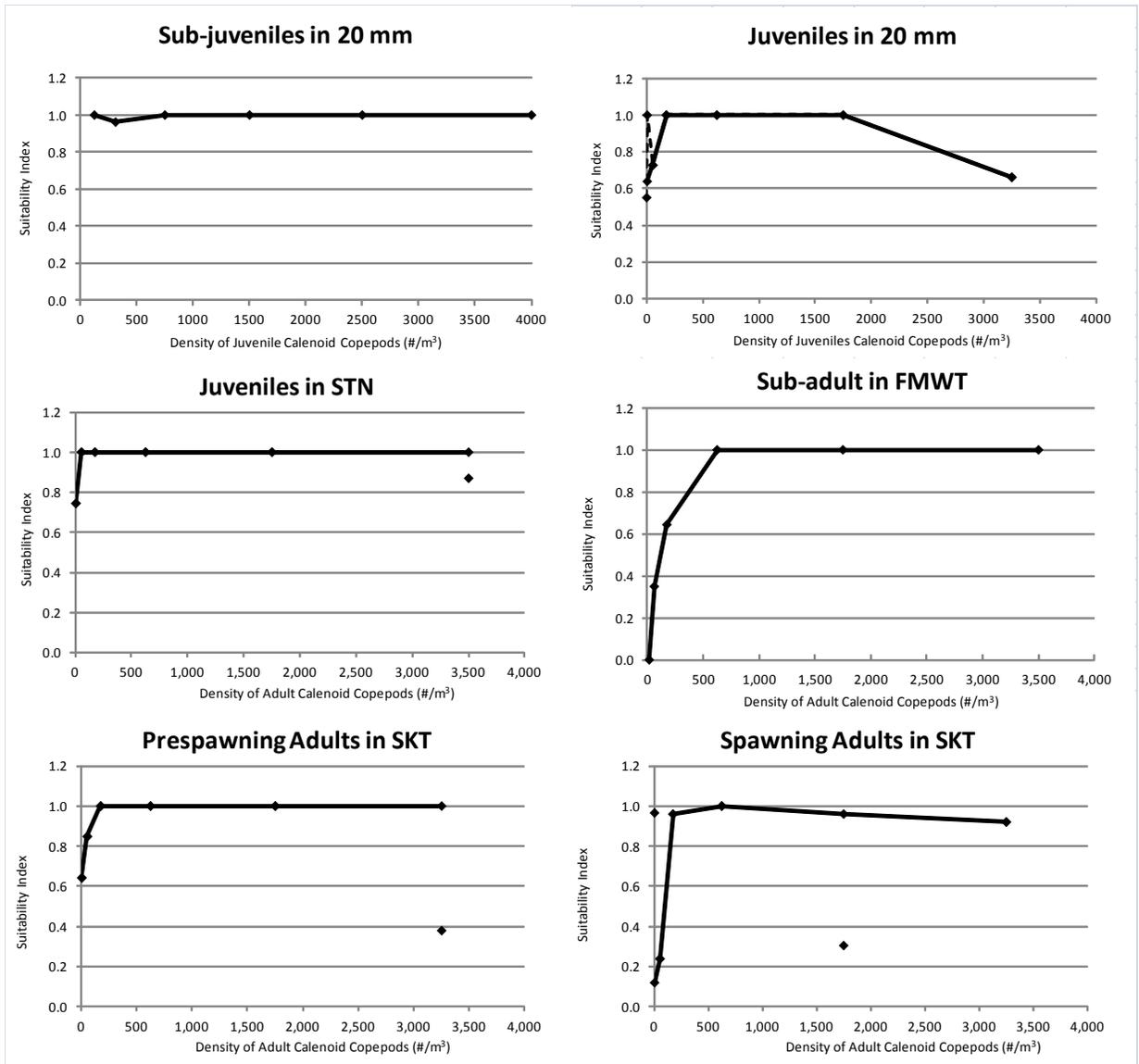


Figure S11. Habitat suitability Index curves for prey density for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

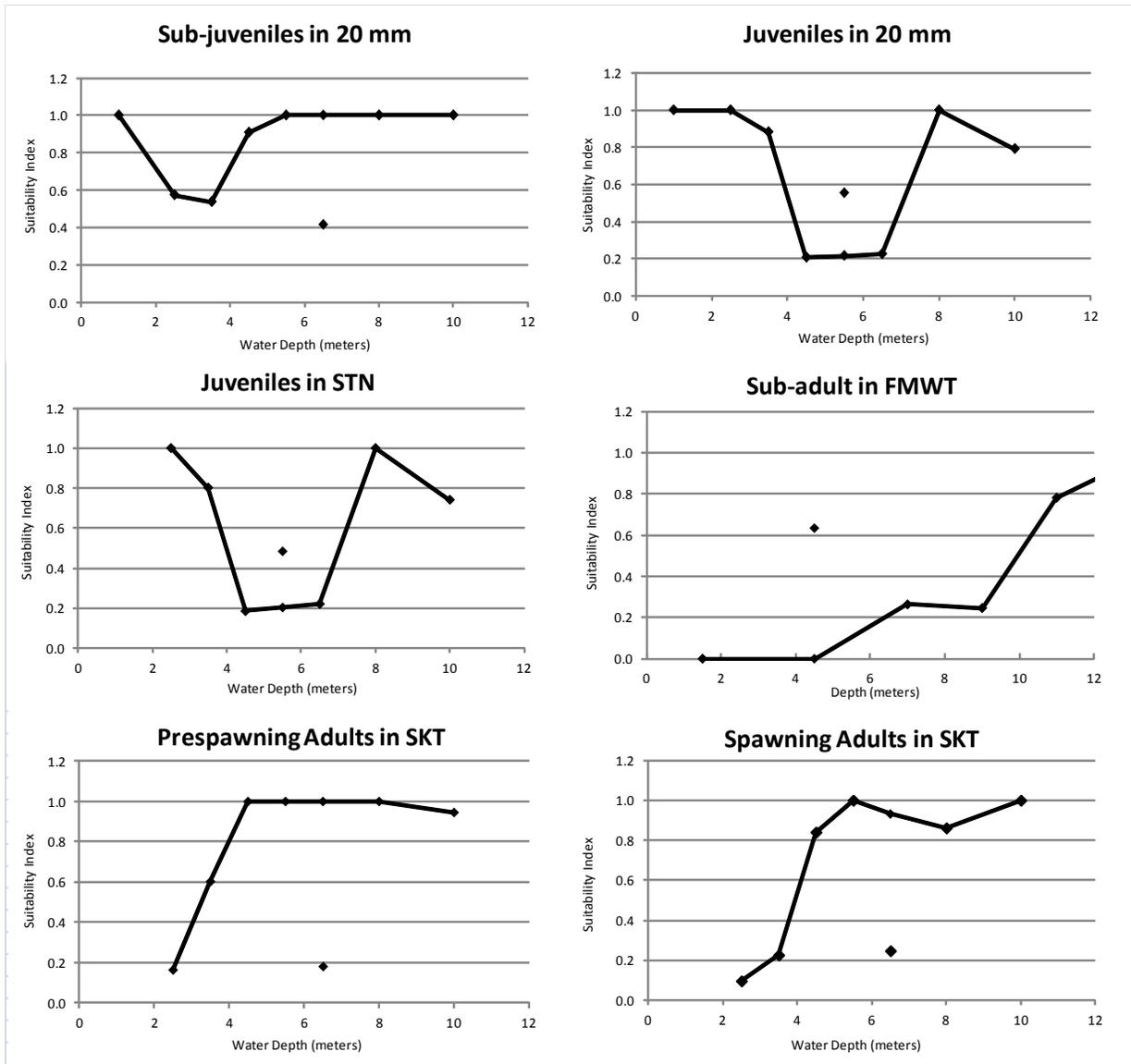


Figure S12. Habitat suitability Index curves for average depth of water for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

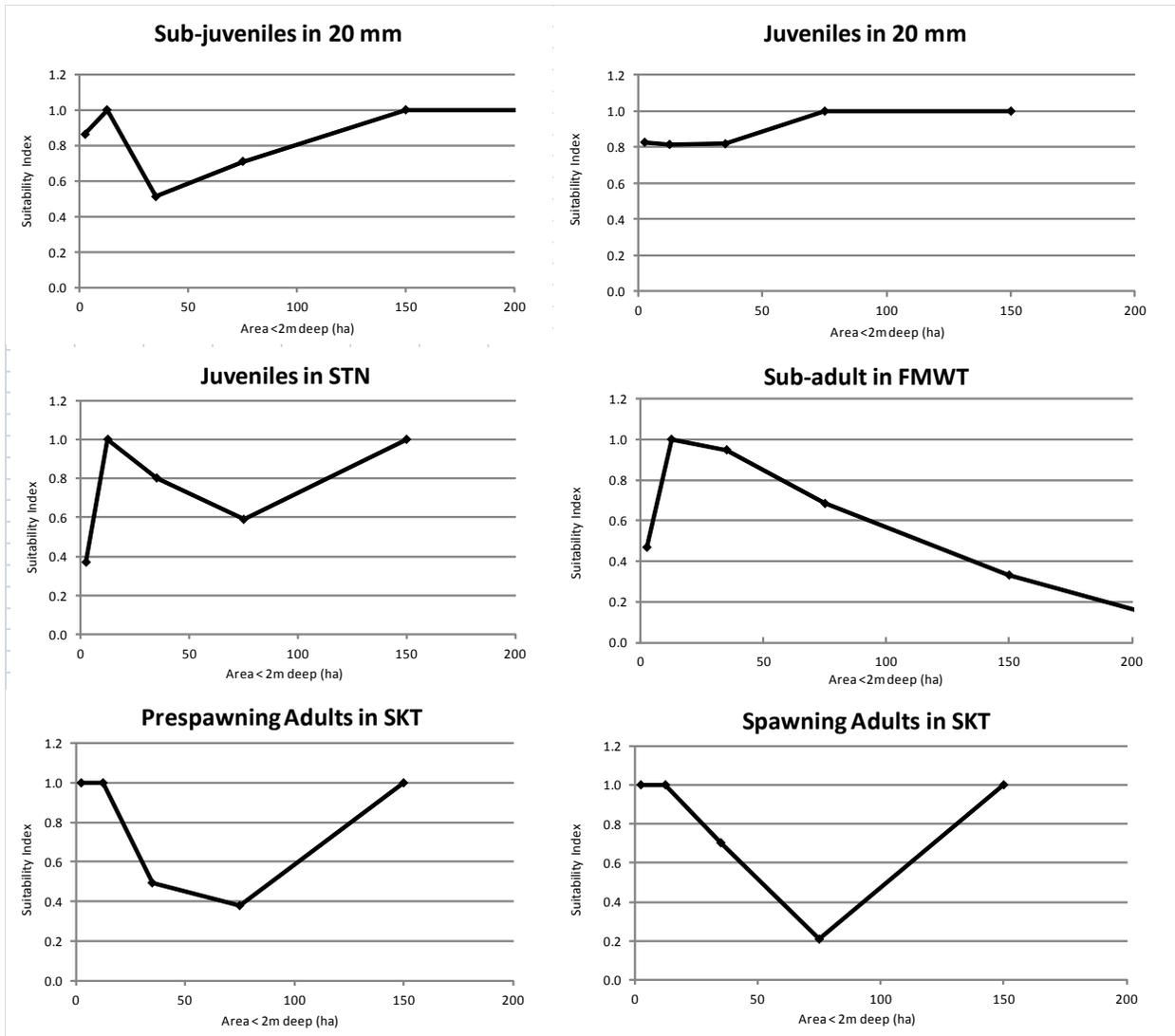


Figure S13. Habitat suitability Index curves for area of shallow (water within 1 km less than 2 meters deep) for various life stages of delta smelt derived from affinity analyses.

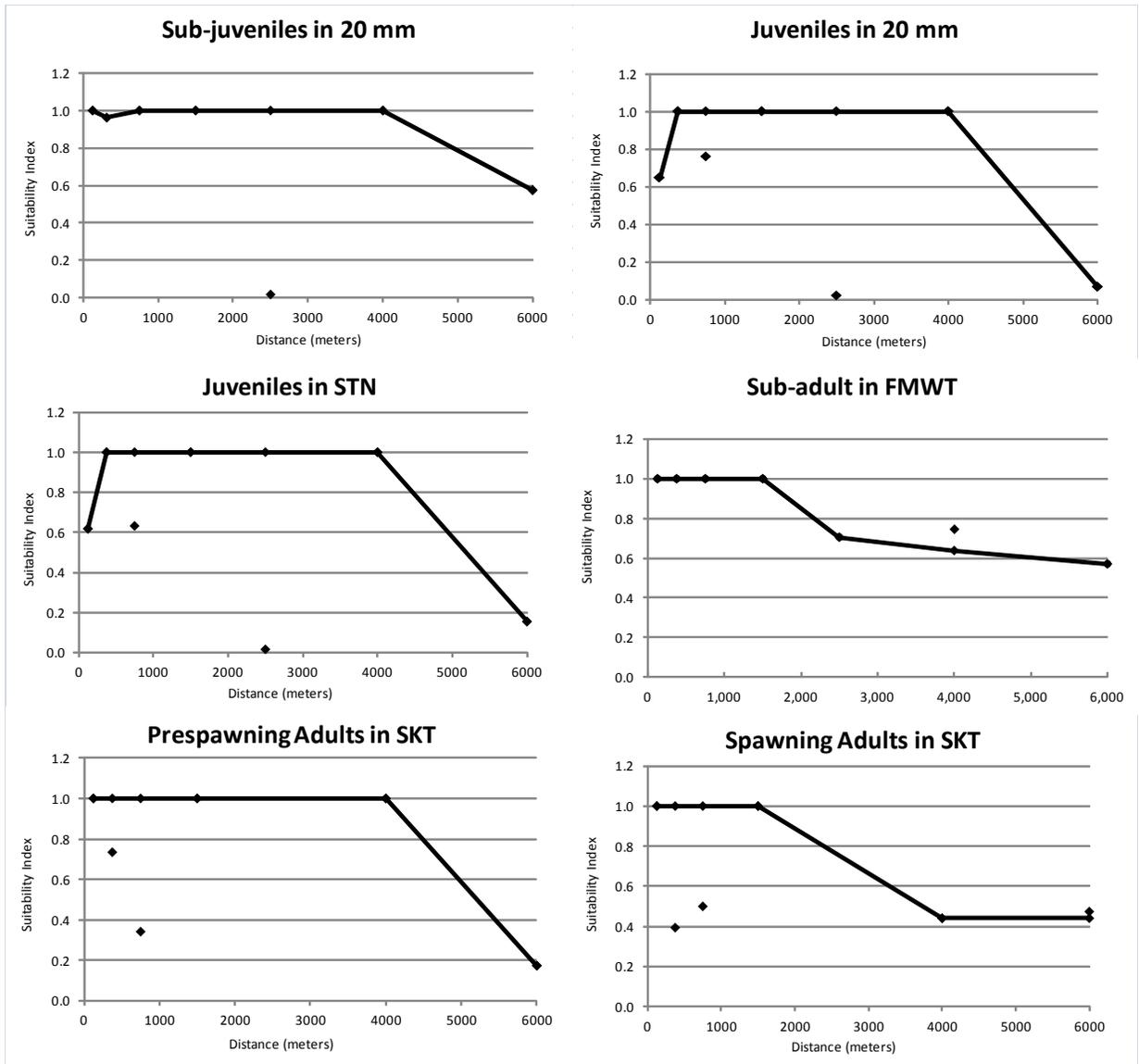


Figure S14. Habitat suitability Index curves for distance to large (>100ha) wetlands for various life stages of delta smelt derived from affinity analyses. Points lying off the line show anomalies in the original data from range segments with a small number of data points.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

3. Tools to Assess the Effect of Changes on Water Supply and Hydrodynamics

3.1 Modeling of trends in outflow and salinity

A hypothesis for the decline of several Bay-Delta fishes is changes to through-Delta flows and the location of the low-salinity-zone. Enright and Culberson (2010) did an extensive review of trends in Delta outflow and salinity. They examined precipitation, outflow, and salinity trends before and after 1968 to discern outflow and salinity response to Central Valley Project (CVP)/State Water Project (SWP) operations (they also include analysis of pre- and post-Suisun Marsh salinity control gate operations, which began in 1988). They conclude that the data do not verify variability reduction; rather, annual and by-month salinity variability is generally greater in the post-project period; and that coefficients of variability for precipitation, outflow, and salinity increased after the projects were initiated. These increases in variability suggests that more powerful mechanisms are at play including land-use changes and climate, which overpower the homogenizing influence of appropriations of water, including those by the CVP/SWP, when considering long-term trends.

This section of the report (1) describes historical outflow, including outflow as measured by the location of X2 over the period of record 1922–2011 and (2) describes some, but not all, causes of identified changes in outflow over time. The period of record is evaluated annually as well as by decade.

The analysis of outflow over time is limited to the seasons that the state and federal fisheries agencies have identified as being potentially important to various aquatic species: fall (September through November) and winter-spring (January through June). The 2008 USFWS Biological Opinion (BiOp) for coordinated operation of the SWP/CVP (OCAP) included a fall outflow experiment (Fall X2 experiment) covering the months September through November (USFWS 2008, pp. 282-283). While acknowledging the uncertainty of benefit, the 2010 Flow Criteria Report also proposed a fall outflow requirement for the months September through November (State Water Board 2010, p. 98). For these reasons, fall outflow (September-November) is analyzed in this report.

The 2010 Flow Criteria Report further proposed a percent of unimpaired flows approach for the winter-spring months, covering January through June (State Water Board 2010, p. 98). They are the same months Jassby *et al.* (1995) used in their statistical analysis of the relationship between winter-spring outflows and longfin smelt abundance. For these reasons, Winter-Spring outflow (January through June) is also analyzed here.

3.1.1 Outflow and Calculated X2 Location (1922-2010)

The 2010 Flow Criteria Report suggests that the magnitude and timing of outflow and the location of the low-salinity zone have changed significantly over time, as evidenced by the difference between calculated unimpaired outflows and actual outflows (State Water Board 2010, pp. 28-33). The analysis contained in the 2010 Flow Criteria Report concludes the difference between unimpaired outflow and actual outflow is a result of increased appropriation

of water from the Bay-Delta estuary and the Sacramento/San Joaquin River watershed. (State Water Board 2010, p. 28). That analysis is not appropriate and the conclusion is not accurate.

Unimpaired flow calculations are informative illustrations of precipitation, and they are used in this report for that purpose. However, as explained in detail below, unimpaired flow calculations are not appropriate estimations of natural outflow. The 2010 Flow Criteria Report fails to account for that fact or the fact that unimpaired flow is a calculation of a hypothetical environment. Unimpaired flow has never existed in our system and cannot be used as a surrogate measure for natural outflows. (DWR 1987, p. 10; *see also*, DWR presentation to State Water Board available on the State Water Board website and incorporated herein by this reference.) To do so would be counter to accepted scientific principles.

Further, it was and would continue to be an error to assume appropriation of water is the sole driver of outflow. As concluded by Enright and Culberson (2010), “seasonal outflow and salinity variability is primarily climate driven.” Enright and Culberson demonstrated that consecutive month outflow differences are consistent with watershed precipitation, suggesting that climate is a more powerful mechanism controlling seasonal variability than water project operations on seasonal and decadal scales.

A further concern with the data cited to support the 2010 Flow Criteria Report is that the grouping of years averaged and used for comparative purposes does not avoid the potential for upstream hydrology to bias the results (State Water Board 2010, pp. 28-32). The analysis presented below evaluates the historical period of record (Water Years 1922 to 2010) and compares this period to the predevelopment era, providing a factual and scientifically sound basis for discussion.

3.1.1.1 Data and Methods

Table 1 summarizes the data used for this trends analysis. The analysis uses monthly flow time series in units of cubic feet per second (cfs.) for the available period of record from October 1921 through September 2010 (Water Years 1922 to 2010). All references to years in this study are to water years (October 1 through September 30 of the calendar year in which it ends) unless otherwise noted. These time series were used to compute annual time series in units of thousand acre-feet (TAF) per year or million acre-feet (MAF) per year. These time series were also used to create 12 monthly data series (*e.g.*, a January series, a February series, etc.) where successive values are 1 year apart.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

Table 1 Data Utilized in Trends Analysis

Data Record	Period of Record	Source
Net Delta Outflow	October 1921 – September 1929	DWR BDO
	October 1929 – September 2010	DAYFLOW
Sacramento River at Freeport	October 1990 – September 2010	DAYFLOW
Yolo Bypass	October 1990 – September 2010	DAYFLOW
San Joaquin River at Vernalis	October 1990 – September 2010	DAYFLOW
Mokelumne River below Woodbridge	October 1990 – September 2010	DAYFLOW
Cosumnes River at Michigan Bar	October 1990 – September 2010	DAYFLOW
Miscellaneous Stream Flow	October 1990 – September 2010	DAYFLOW
Delta Net Consumptive Use	October 1990 – September 2010	DAYFLOW
Delta Exports	October 1990 – September 2010	DAYFLOW
Unimpaired Flows	October 1990 – September 2010	DWR BDO
Sacramento River @ Shasta	October 1990 – September 2010	CDEC
American River @ Nimbus	October 1990 – September 2010	CDEC
Feather River @ Thermalito	October 1990 – September 2010	CDEC
Yuba River @ Marysville	October 1990 – September 2010	CDEC
Sacramento Accretions	October 1990 – September 2010	Calculated
Unimpaired Sacramento Accretions	October 1990 – September 2010	Calculated
X2 Location	October 1921 – September 2010	Calculated

BDO- Bay-Delta Office

CDEC – California Data Exchange Center (DWR 2011)

Calculated unimpaired flows include: Sacramento Valley, Sacramento River @ Red Bluff, Feather River, Yuba River, American River, San Joaquin Valley, East Side Streams, and In-Delta Consumptive Use

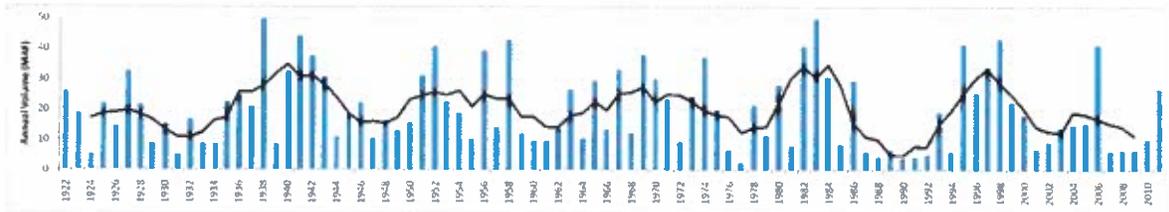
The primary source of historical Delta inflow and outflow data is the DAYFLOW database (DWR 2012). Monthly averages are computed from daily values provided in the database. Historical flows prior to October 1929 are based on a joint DWR-Bureau of Reclamation (1958) hydrology study and provided as monthly averages by the staff of DWR's Bay-Delta Office. Historical Eastside inflow is computed as the sum of historical river flows from the Mokelumne, Cosumnes, and miscellaneous streams. Historical Delta outflow, as reported in the DAYFLOW database, is a computed value based on water balance. In reality, Delta outflow is tidally influenced and fluctuates over daily diurnal flood-ebb cycles and over bimonthly spring-neap cycles. For example, outflow during summer tidal cycle can vary in direction and amount from 330,000 cfs. upstream to 340,000 cfs. downstream (Delta Atlas, 1993).

3.1.2 Annual Delta Outflow (1922–2010)

Annual Delta outflow shows no clear long-term time trend. Fox *et al.* (1990) found no statistically significant trend in annual Delta outflow between 1922 and 1986. The investigators concluded that precipitation had increased faster than water use within the watersheds. They noted that other factors, including imports, the redistribution of groundwater, and changes in runoff patterns, may have balanced the increase in water use within the watersheds.

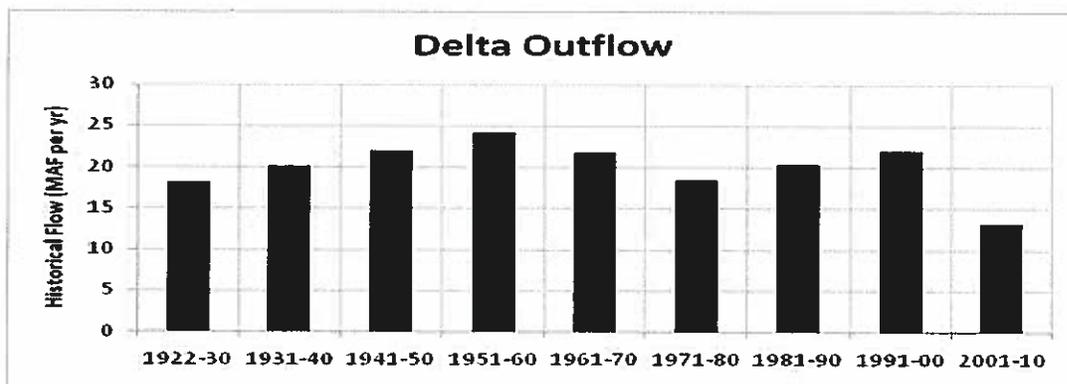
As shown on Figure 1, visual inspection suggests no statistically significant long-term trend in Delta outflow (shown as the blue bars) from 1922 and 2010. The black line shows a 5-year center-weighted average outflow. A Sen’s nonparametric estimate of the long-term trend was conducted. A Mann-Kendall test, a two-sided test performed at the 95 percent confidence level, confirms that no statistically significant time trend exists.

Figure 1 Annual Variation in Outflow (TAF) showing no statistically significant trend over time.



To further characterize the outflow time series, Delta outflow is shown as decadal averages on Figure 2. The figure shows that decadal average outflows have varied, following no particular trend. However, outflow decreased in the most recent decade (2001–2010), the decade often described as the Pelagic Organism Decline (POD) period, compared to the previous decade (1991–2000), the pre-POD period and the second wettest period of record.²

Figure 2 Delta outflow by decade (1922–2010) showing no particular long term trend and a decrease in outflow in the most recent decade (the POD period) compared to the previous decade (the pre-POD period).

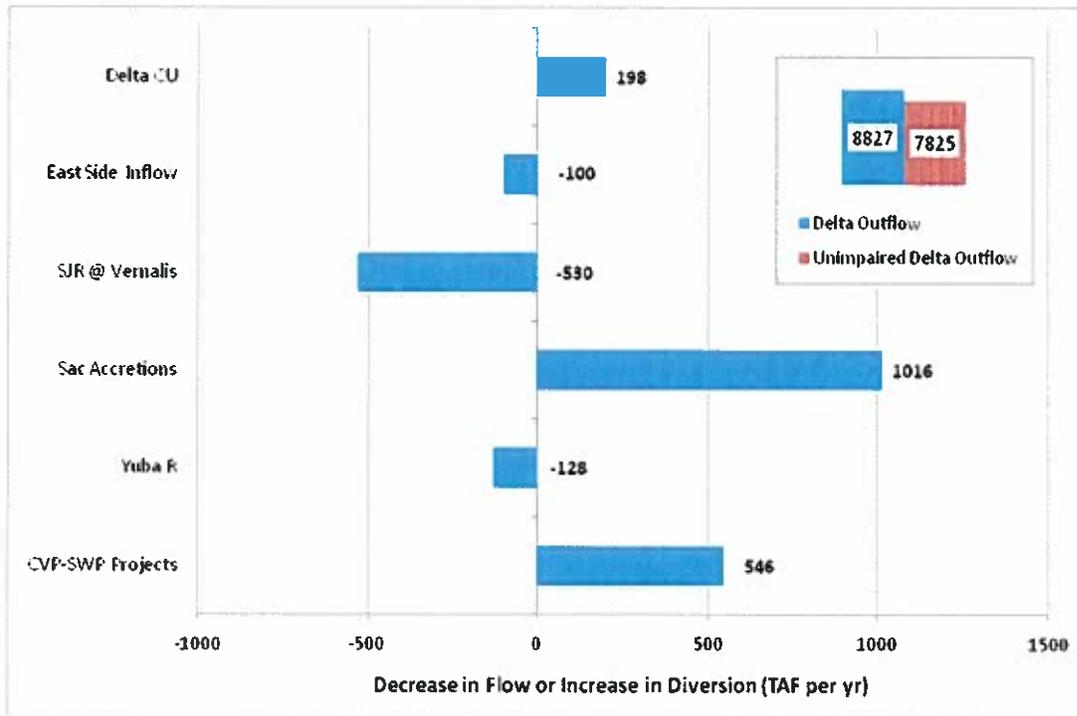


In an effort to understand the reasons for the decrease in outflow from the prior decade (1991–2000) to the recent decade (2001–2010), this analysis evaluates changes in inflows to the Delta and increases in water diversions, by source, both upstream and in-Delta.

² The 1991-2000 is the second wettest period of record based on the 8-River index.

Figure 3 demonstrates that annual outflow reduction is primarily the result of dryer hydrologic conditions between the prior decade (1991–2000) to the most recent decade (2001–2010). The vertical bar chart inset in the top right-hand corner of the figure demonstrates that the difference in outflow is explained in large part by the difference in unimpaired outflow (i.e. the unimpaired outflow reduction [red bar at 7,825 TAF/year] accounts for a majority of the outflow reduction [blue bar at 8,827 TAF/year]). In other words, the outflow reduction between decades is primarily the result of dryer hydrologic conditions; however, water management also contributed to the outflow reduction. The horizontal blue bars in the main body of the figure represent normalized contributions by individual hydrologic drivers towards the decrease in annual outflow between decades. The blue bars in the main body of the figure represent the changes in outflow other than hydrology, which is the largest driver of changes in outflow. These horizontal blue bars sum to the difference between the vertical bars. The figure shows that, after the reduction in unimpaired outflow, the reduction in Sacramento Valley accretions (1,016 TAF/year) is the most significant hydrologic factor explaining the decrease in outflow between the 2 decades. In-Delta appropriations by the CVP and SWP have a much smaller contribution to the outflow reduction (546 TAF/year); this contribution aggregates effects of in-Delta appropriations by the CVP and SWP and inflows from the Sacramento River (below Shasta), the Feather River, and the American River.

Figure 3 Contributions to decrease in annual outflow. Horizontal bars indicate sources of the change in outflow between decades. The majority of the difference in outflow between these two decades is due to differences in natural hydrology as measures by unimpaired outflow. Reductions in Sacramento accretions are the next largest contributor, followed by increases in CVP/SWP appropriations.



3.1.3 Calculated X2 Location (1922–2010)

The 2010 Flow Criteria Report focuses on fall (September through November) and winter-spring (January through June). As a result, this analysis of X2 location focuses on the data from these two seasons over the historical period (1922-2010).

The location of X2³ is determined by a variety of factors. Freshwater from the upstream watersheds mixes with salty ocean water in the Delta. This freshwater flow (*i.e.*, Delta outflow) pushes the freshwater-seawater interface downstream; therefore, changes in Delta outflow (annual volumes as well as seasonal timing) affect the location of X2. Long-term changes in tidal energy, including sea level rise, influences how effectively freshwater flow pushes seawater downstream. Geometry of the land-water interface plays a key role in determining the tidal prism, amplitude, and excursion. Therefore, historical changes, including, but not limited to, changes in floodplains, channel configuration, bathymetry, and depth, affect long-term trends in the position of X2. Operation of water facilities such as the Suisun Marsh salinity gates and the Delta Cross Channel influence the flow paths within the Bay-Delta, therefore, also affect X2 positions.

The analysis presented in this paper is limited in its ability to evaluate the multiple factors that affect long-term X2 trends. As described in the following section, the X2 locations described in this study were estimated from flow data and therefore capture the influence of Delta outflow only. Therefore, the trend analysis does not reflect possible changes associated with sea-level rise, Delta island flooding, etc. It is anticipated that further analysis will be undertaken that will utilize measured salinity data to evaluate long-term X2 trends and, therefore, will reflect changes associated with other factors.

3.1.3.1 Data and Methods

The metric used in this study to evaluate long-term X2 trends is the calculated monthly average X2 location. The Delta outflow data described in Table 1 were used to estimate time series of the monthly average X2 location. These time series were also used to create 12 monthly data series (*e.g.*, a January series, a February series, etc.) where successive values are 1 year apart. A time series of the historical monthly average X2 location was developed for this trend analysis using the Kimmerer-Monismith (K-M) equation (Jassby *et al.* 1995). The K-M equation predicts average X2 location as a function of current month Delta outflow and previous month X2 location. The early historical Delta outflow time series includes several months when the value was negative. Since the K-M equation is a function of the common log of Delta outflow,

³ The authors of this paper are not aware of any studies that conclude that the two part per thousand isohaline location (X2) is preferred by native fish over, for example, the one part per thousand or three parts per thousand isohaline positions. The resident native fish are largely adapted to a wide range of salinities (euryhaline). Instead, management of the X2 location was believed to create hydrodynamic conditions that maintain the “entrapment zone” in a location that is conducive to successful fish rearing (Jassby *et al.* 1995). References in this paper to shifts in the X2 location, therefore, should be understood to refer to shifts in hydrodynamic conditions and are not intended to suggest that any absolute salinity level has been found to be a central driver to fishery success.

the equation is not defined when outflow is less than 1 cfs. Therefore, an alternate approach was developed and utilized to estimate the X2 location when the K-M equation is not valid (Hutton 2011). As the X2 location used in the comparison and trend analysis reported below is a calculated location, differences may occur between the calculated X2 locations and the actual location, particularly in low outflow years after 1990.

3.1.4 Fall X2

The 2010 Flow Criteria Report cited Feyrer *et al.* (2007, 2011), (the latter of which was still in review at the time), for the conclusion that the average X2 location during fall has moved upstream, resulting in a corresponding reduction in the amount and location of suitable delta smelt abiotic habitat, as estimated by the X2 location (State Water Board 2010, p. 108). The Public Water Agencies reviewed these analyses and concluded that:

- Fall outflows were higher than unimpaired flows during the period 1956 to 1987 because the reservoirs were operating and making releases to reach mandatory reduced storage levels before the next rainy season. During this period, water demand throughout the watershed and in the Delta was developing so reservoir releases to create flood control space kept the Delta artificially fresh.
- The relevance of the time periods used in the 2010 Flow Criteria Report and in Feyrer *et al.* (2007, 2011) is not clearly articulated nor justified. The hydrological conditions that existed in the 1950s thru 1980s were highly altered, as further evidenced by the artificially fresh Delta in the fall, which to a certain extent flattened the hydrograph rather than supported variability.
- The actual trends in the location of X2 in fall are different than those presented in the 2010 Flow Criteria Report. The X2 location is, in fact, further downstream in the Delta (the Delta is fresher) in September, and about the same in October, compared to conditions before Shasta Dam was constructed.

The historical data indicate that the calculated X2 location early in the fall has been moving west (Delta becoming fresher) over time, with a flattening of that trend in more recent decades. The X2 data for the months August and September show the location of X2 trending closer to the San Francisco Bay, a downward trend (Figures 4 through 7). The month of August is added to this analysis because X2 in August affects X2 in September. A Sen's nonparametric estimate of the long-term trend was conducted, showing downward trends in August and September of 1.2 and 0.7 kilometers per decade, respectively. A Mann-Kendall test confirms the statistical significance of these trends.

Figure 4 Calculated X2 location in August 1922–2010, showing a statistically significant downward trend of 1.2 kilometers per decade over the time period.

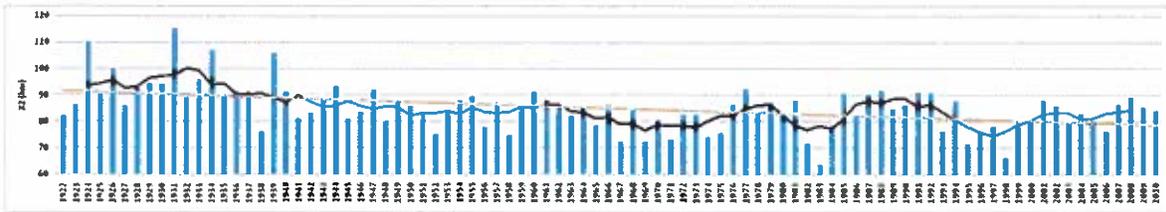


Figure 5 Calculated X2 location in August by decade (1922–2010).

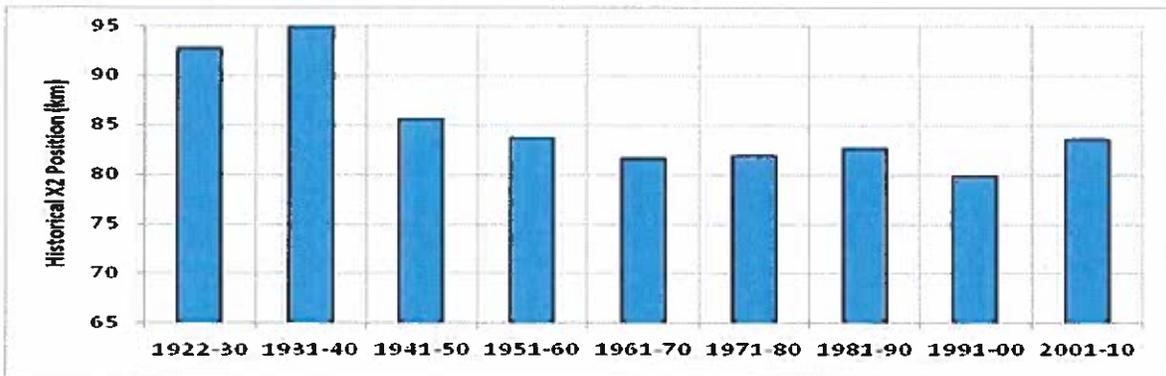


Figure 6 Calculated X2 location in September 1922–2010, showing a statistically significant downward trend of 0.7 kilometers per decade over the time period.

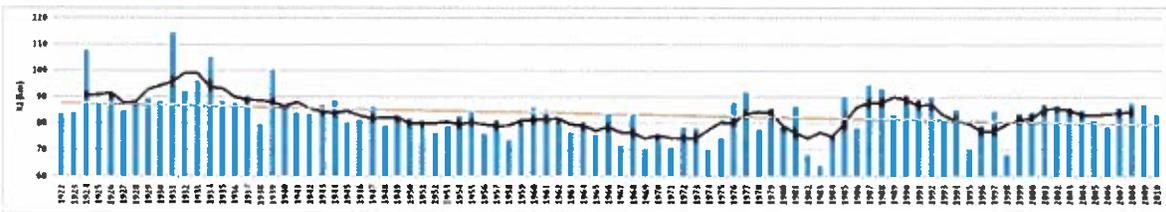
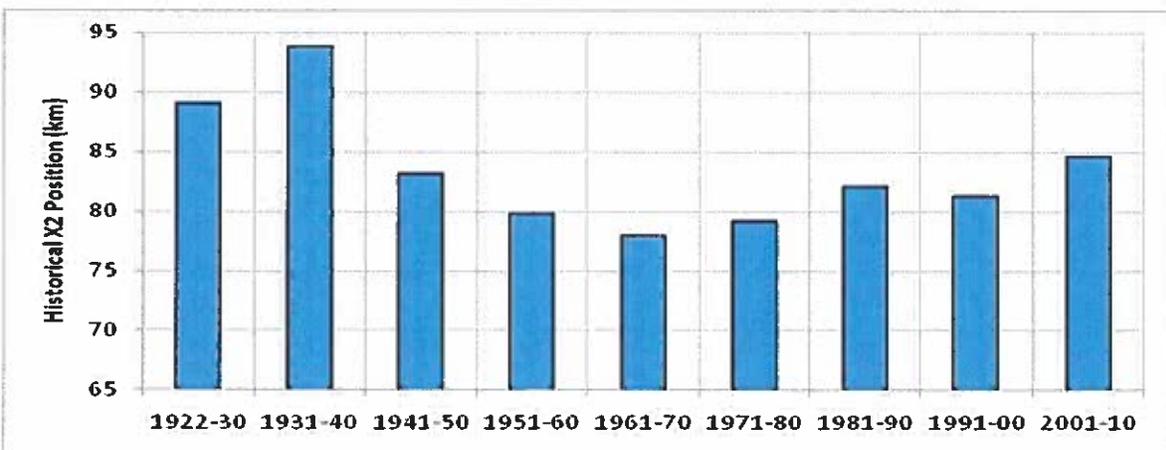


Figure 7 Calculated X2 location in September by decade (1922–2010).



Figures 8 and 9, upon visual inspection, indicate no long-term trend in the position of X2 in Octobers. A Mann-Kendall test confirms that no significant long-term trend exists. Figures 10 and 11 for the month of November show a different trend, with increasing X2 over time. A Sen’s nonparametric estimate of the long-term trend was conducted, resulting in an increasing trend of 0.5 kilometer per decade. A Mann-Kendall test confirms the statistical significance of this trend.

Figure 8 Calculated X2 location in October 1922–2010, showing no significantly significant trend in salinity over the time period.



Figure 9 Calculated X2 location in October by decade (1922–2010).

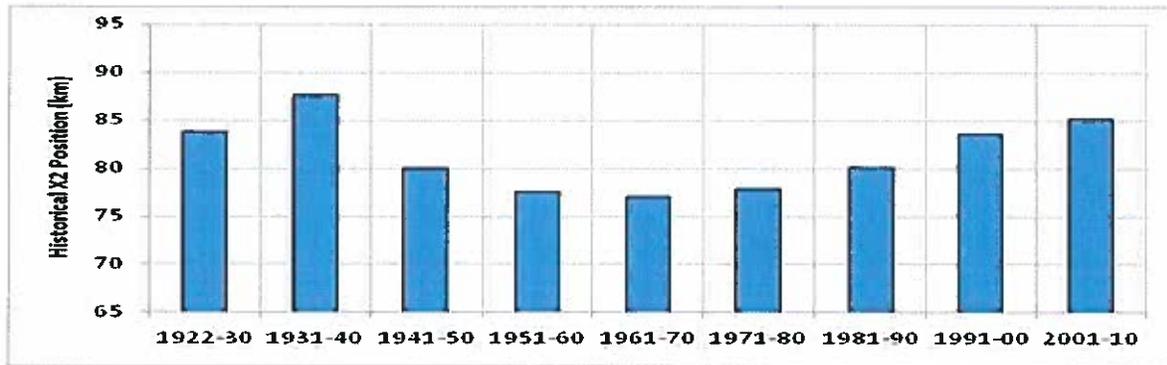


Figure 10 Calculated X2 location in November 1922–2010, showing a statistically significant increasing trend of 0.5 kilometers per decade over the time period.

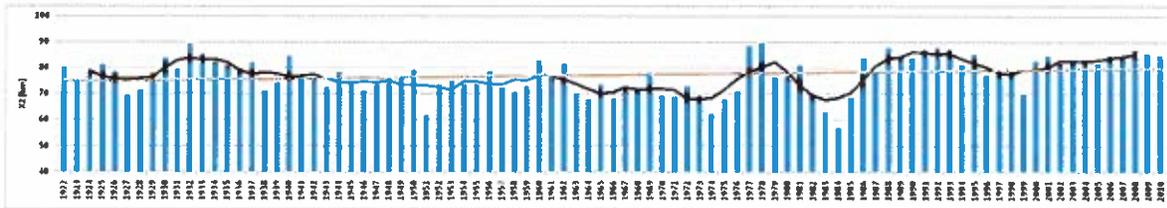


Figure 11 Calculated X2 location in November by decade (1922–2010).

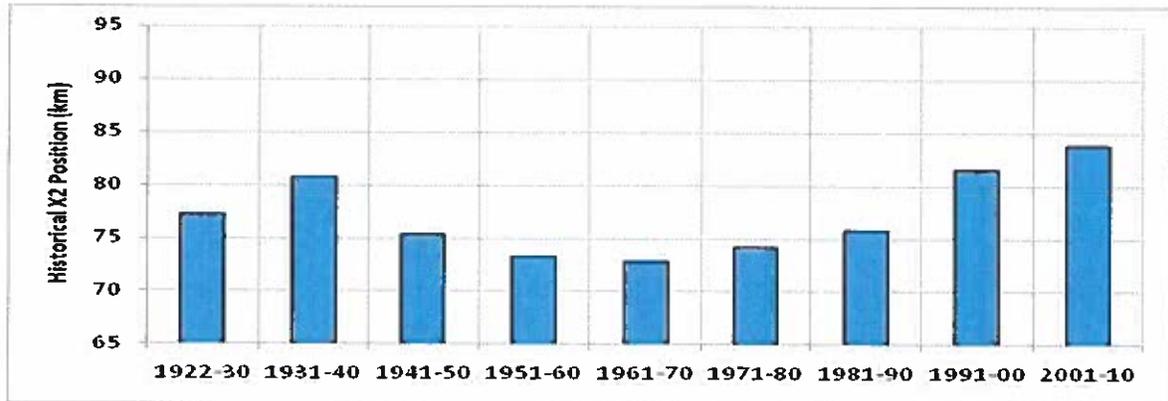
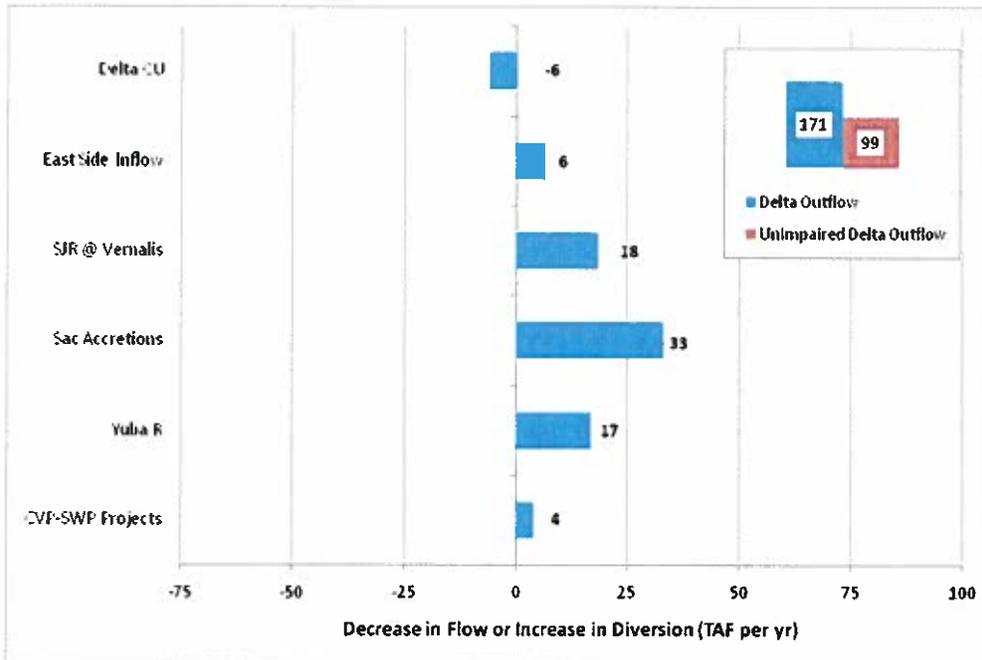


Figure 12 demonstrates that the September outflow reduction is primarily the result of dryer hydrologic conditions that have occurred between decades, from the prior decade (1991–2000) to the most recent decade (2001–2010). The vertical bar chart inset in the top right-hand corner of the figure demonstrates that the difference in outflow is explained in large part by the difference in unimpaired outflow (i.e., the reduction in unimpaired outflow [red bar at 99 TAF/year] accounts for a majority of the reduction in outflow [blue bar at 171 TAF/year]). However, water management also contributed to the outflow reduction. The horizontal blue bars in the main body of the figure represent normalized contributions by individual hydrologic drivers towards the decrease in annual outflow between decades. These horizontal blue bars sum to the difference between the vertical bars. These horizontal blue bars in the main body of the document represent changes in outflow other than hydrology. The figure shows that, after reduction in unimpaired outflow, the reduction in Sacramento Valley accretions (33 TAF/year) is the next most significant hydrologic factor explaining the decrease in September outflow between the 2 decades. The CVP/SWP Projects appear to have had minimal (4 TAF/year) contribution to reductions in outflow. Increased exports are nearly balanced by increased upstream project reservoir releases.

Figure 12 Contributions to decrease in September Delta outflow (1991-2000 compared to 2001-2010). The majority of the difference in outflow between these two decades is due to differences in natural hydrology as measured by unimpaired outflow. Reductions in Sacramento accretions are the next largest contributor.



Similar to Figure 12, Figures 13 and 14 identify the hydrologic factors that drive the decrease in October and November outflow from the prior decade (1991–2000) to the most recent decade (2001–2010), respectively. The vertical bars on Figure 13 show that unimpaired flow was higher in 2001–2010 than in 1991–2000 (red bar at -14 TAF/year). The figure shows that the reduction in Sacramento Valley accretions (93 TAF/yr) and San Joaquin River inflow at Vernalis (40 TAF/year) were the most significant factors in explaining the decrease in October outflow between the 2 decades. The CVP/SWP Projects actually contributed to higher outflow in 2001–2010 (-57 TAF/year), i.e., increased exports were more than fully balanced by increased upstream project reservoir releases. The vertical bar chart inset in the top right-hand corner of Figure 14 demonstrates that the difference in November outflow is explained in large part by the difference in unimpaired outflow; that is, the reduction in unimpaired outflow [red bar at 107 TAF/year] accounts for a majority of the reduction in outflow [blue bar at 136 TAF/year]. The horizontal blue bars in the main body of the figure represent normalized contributions by individual hydrologic drivers towards the decrease in annual outflow between decades. These horizontal blue bars sum to the difference between the vertical bars. These horizontal blue bars in the main body of the document represent changes in outflow other than hydrology. The figure shows that, after reduction in unimpaired outflow, no single hydrologic factor stands out in explaining the decrease in November outflow between the 2 decades. In other words, while water management also contributed to the outflow reduction between decades that reduction is primarily the result of dryer hydrologic conditions.

Figure 13 Contributions to decrease in October Delta outflow (1991-2000 compared to 2001-2010). Unimpaired flow was higher in the most recent decade. Reduction in Sacramento Valley accretions and San Joaquin River inflow at Vernalis were the most significant factors in explaining the decrease in October outflow between the two decades. CVP/SWP Projects contributed to higher outflow in 2001-2010.

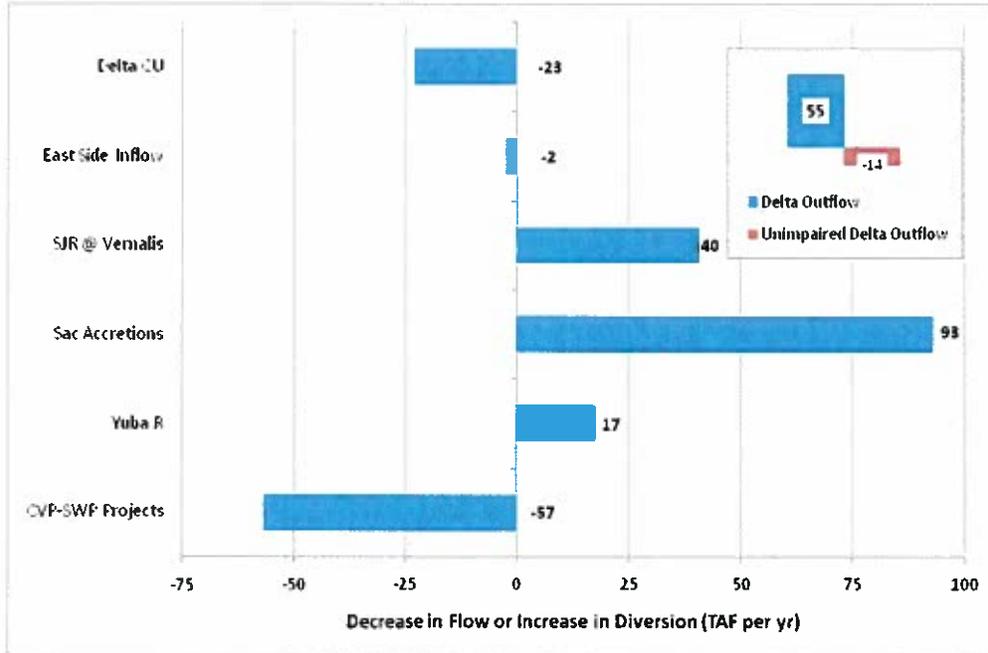
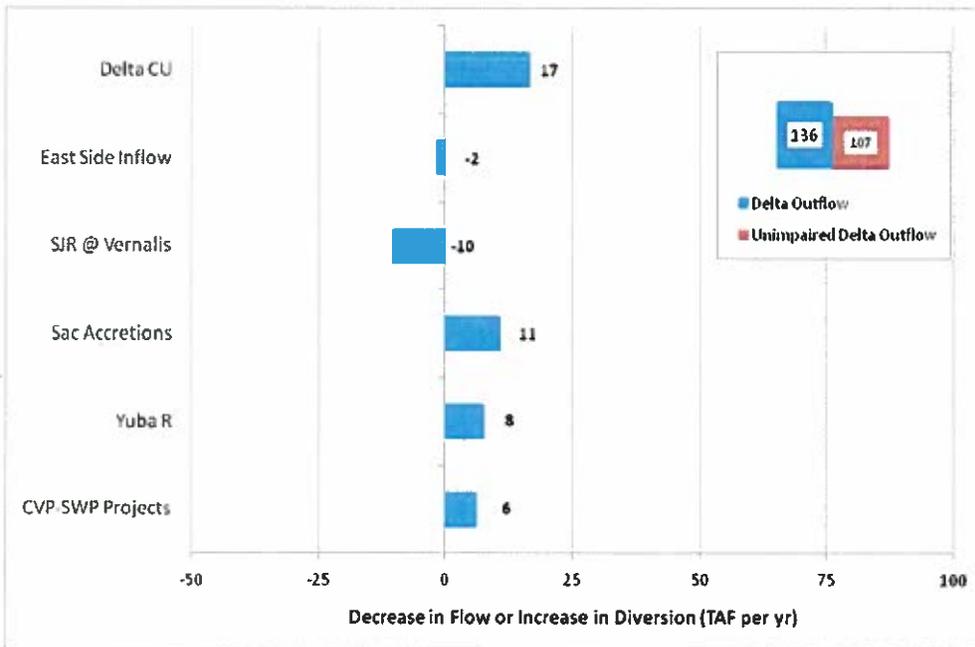


Figure 14 Contributions to decrease in November Delta outflow (1991-2000 compared to 2001-2010). The difference in November outflow is explained in large part by the reduction in unimpaired outflow. After reduction in unimpaired outflow, no single hydrologic factor stands out in explaining the decrease in November outflow between the two decades.



3.1.5 Winter-Spring X2

The 2010 Flow Criteria Report proposed a percent of unimpaired flow approach to managing outflow from January through June (State Water Board 2010, p. 98). The primary justification for this recommendation was the statistical correlation between winter-spring (January-June) outflow (X2) and longfin smelt abundance (State Water Board 2010, pp. 100-108). A secondary rationale was the existence of various other statistical correlations between abundance of several non-Endangered Species Act listed species and outflow (X2) during various months within the January-June (winter-spring) timeframe (State Water Board 2010, pp.100-108). A third rationale was a citation to Bunn and Arthington (2002) and their four principles that generally describe how flow affects aquatic biodiversity, although the 2010 Flow Criteria Report did not explain the potential applicability of those principles to the Bay-Delta estuary (State Water Board 2010, p. 100). To support the conclusion that outflow (X2) has changed over time, creating an increasingly unnatural flow pattern, the 2010 Flow Criteria Report made several comparisons between actual outflow and unimpaired outflow over various time periods: 1956–1987, 1988–2009, and 2000–2009 (State Water Board 2010, p. 104).

There are several observations in the 2010 Flow Criteria Report regarding the analysis of Winter-Spring X2 patterns that are particularly relevant and worth reconsidering.

- It is not appropriate or meaningful to average the winter months (January-March) and the spring months (April-June) together for the purpose of identifying trends in outflow. The hydrology between winter and spring is in stark contrast, as are the life stages and biological requirements of the fishes in the two seasons. The inflow and diversion patterns are also quite different in winter compared to spring.
- The time periods selected (1956–1987, 1988–2009, and 2000–2009) for comparative purposes in the 2010 Flow Criteria Report raise a number of concerns. It is unclear how natural hydrology was accounted for in the selection of averaging periods. This lack of clarity is a concern as natural hydrology can skew the results of a data analysis, thereby suggesting changes in water consumption that may not exist. The biological relevance of the time periods selected (1956 and later) is also questionable because these periods represent highly altered physical conditions in the Delta and are, therefore, not related to “natural” or undeveloped conditions. It is also unclear why the entire hydrologic record was not used in the analysis.
- As mentioned previously and as discussed in more detail below, unimpaired flows are a calculation of artificial conditions. The Delta and the fishes within the Delta have never experienced unimpaired outflow. It is, therefore, inappropriate to compare the artificial unimpaired flow calculation to actual historical outflow conditions and conclude that a change has occurred.
- By averaging two entirely different seasons over several decades, the trends in the position of X2 are obscured. The analysis considers data at several different scales and then asserts that differences in the calculated X2 locations are the proximate cause.

When January-June data are considered over the entire hydrologic record, an eastward movement of the X2 line does appear to have occurred through time (Figure 15). This outcome is expected because one of the historic purposes of the reservoirs was to capture and store water in the winter and spring (thereby reducing outflow) and to facilitate releases of freshwater in the summer and fall.

Figure 15 Calculated X2 location in January through June 1922–2010 showing X2 trending eastward over time due to construction and operation of reservoirs designed to capture winter and spring flows to reduce flooding and to store water for release later in the year.

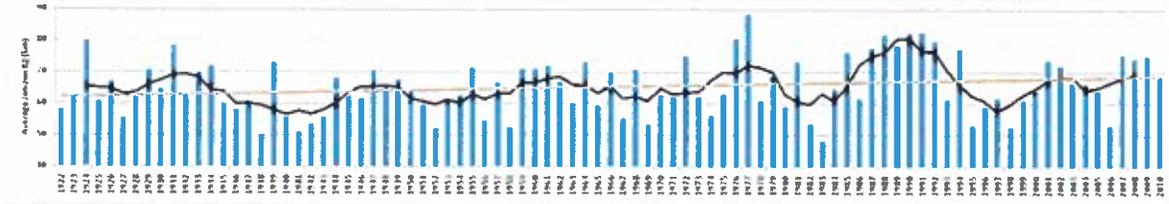
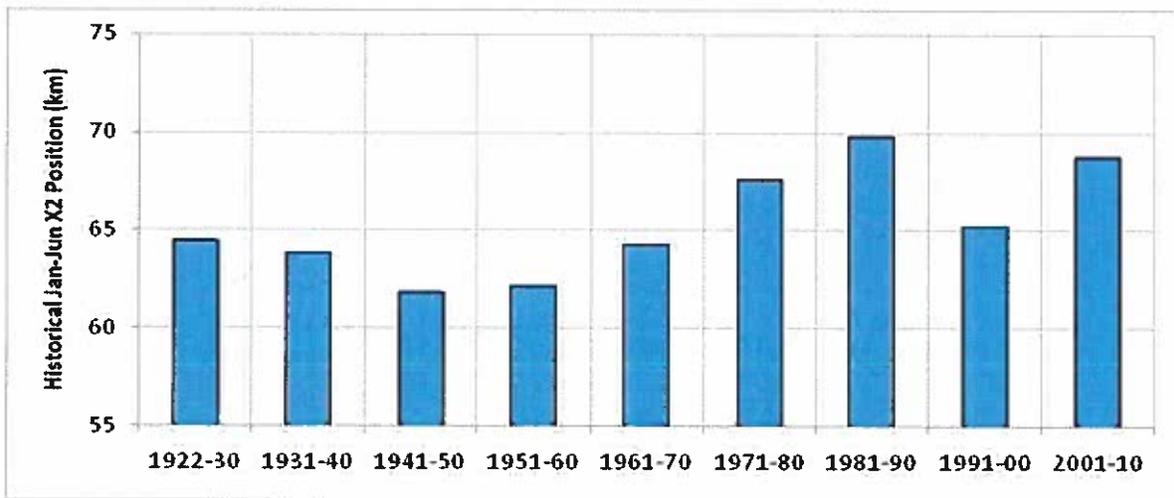


Figure 16 Calculated X2 location in January through June by decade (1922–2010). Calculated X2 location moved eastward after major reservoirs were constructed in the 1940s and 1950s; however, the increase has not been steady over time.



Figures 15 and 16 are mirroring the gross scale of the 2010 Flow Criteria Report, which makes identifying seasonal trends difficult. Therefore, this analysis also considers changes in the calculated X2 location by month. As spring is generally considered the most biologically important season for fishes, Figures 17 through 19 show the monthly X2 location for April, May, and June. The April data show that the calculated X2 location in 2001–2010 was comparable to the decades 1971–1990, but more easterly than 1991–2000. Data from the more recent two decades shows May and June to be fresher than they were in the immediately prior three decades (1971–1990) and are comparable to the decade 1961–1970.

Figure 17 Calculated X2 location in April 1922–2010. Calculated X2 location in 2001–2010 was comparable to the decades 1971–1990, but more easterly than 1991–2000.

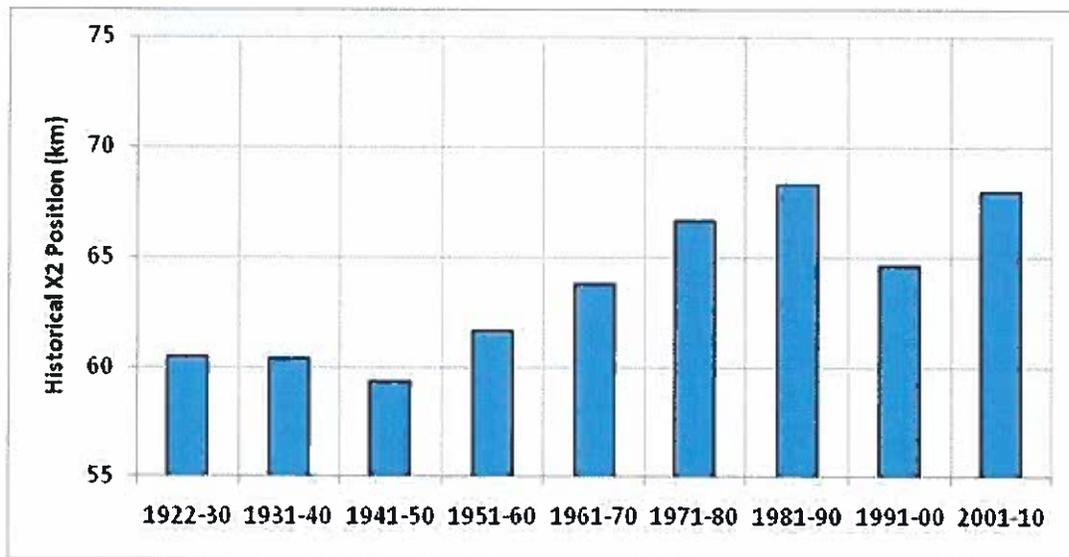


Figure 18 Calculated X2 location in May 1922–2010. The most recent two decades (1991–2010) were fresher than the immediately prior three decades (1971–1990) and were comparable to the decade 1961–1970.

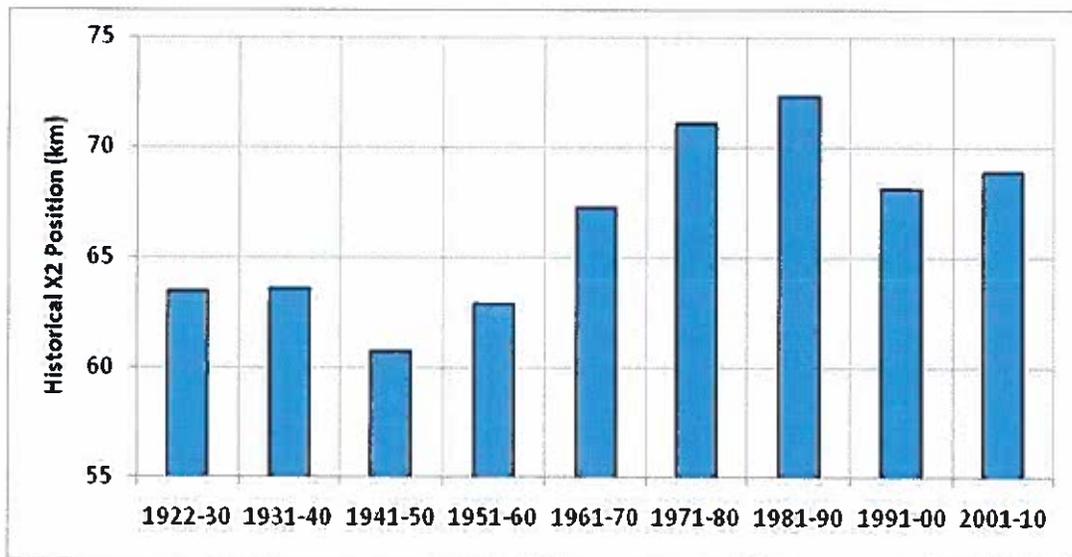
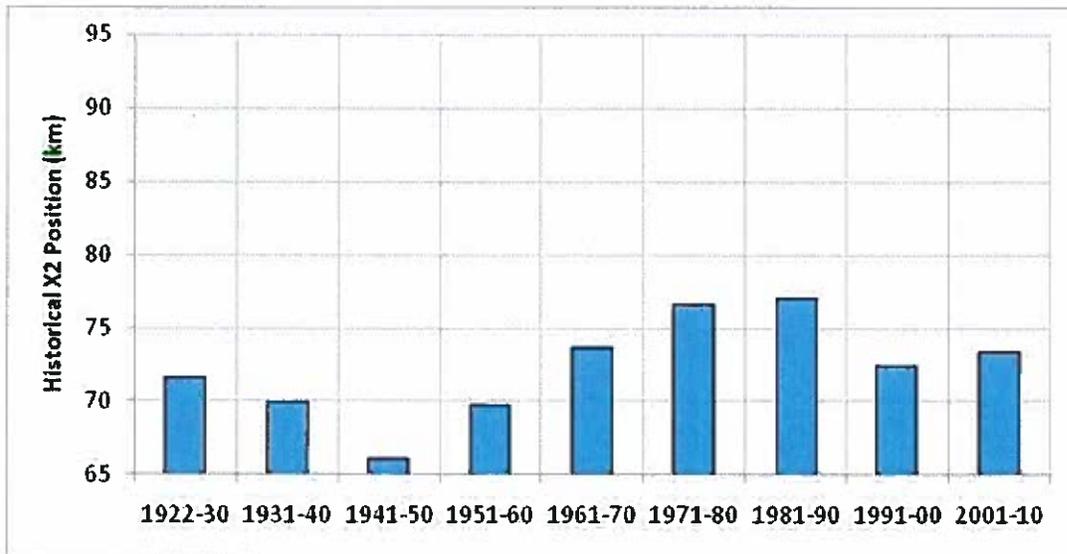


Figure 19 Calculated X2 location in June 1922–2010. The most recent two decades (1991–2010) were fresher than the immediately prior three decades (1971–1990) and were comparable to the decade 1961–1970.



Figures 20 through 22 show the monthly X2 location for January, February, and March. In these months, the most recent decade (2001–2010) is most comparable to the decade 1981–1990. In the most recent decade (2001–2010) X2 has on average been further upstream than in the prior decade (1991–2000).

Figure 20 Calculated X2 location in January 1922–2010. The most recent decade (2001–2010) is most comparable to the decade 1981–1990. In the most recent decade (2001–2010) X2 was further upstream on average than in the prior decade (1991–2000).

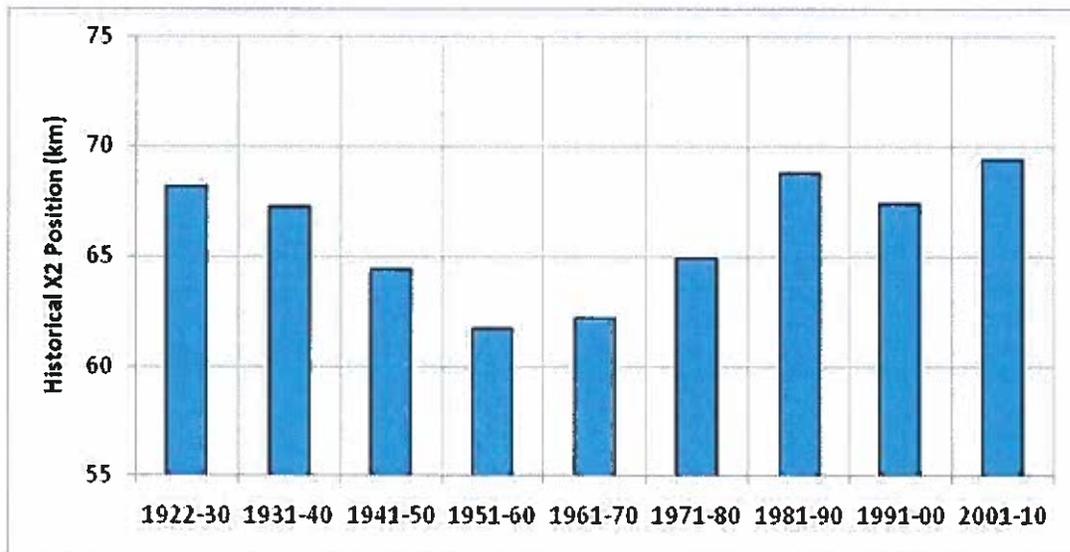


Figure 21 Calculated X2 location in February 1922–2010. The most recent decade (2001–2010) is most comparable to the decade 1981–1990. In the most recent decade (2001–2010) X2 was further upstream on average than in the prior decade (1991–2000).

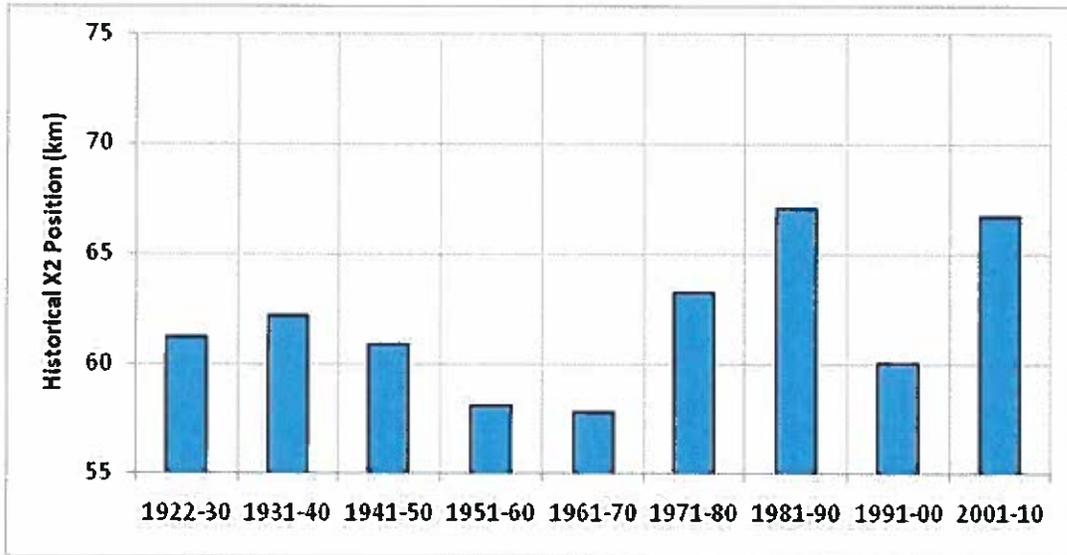
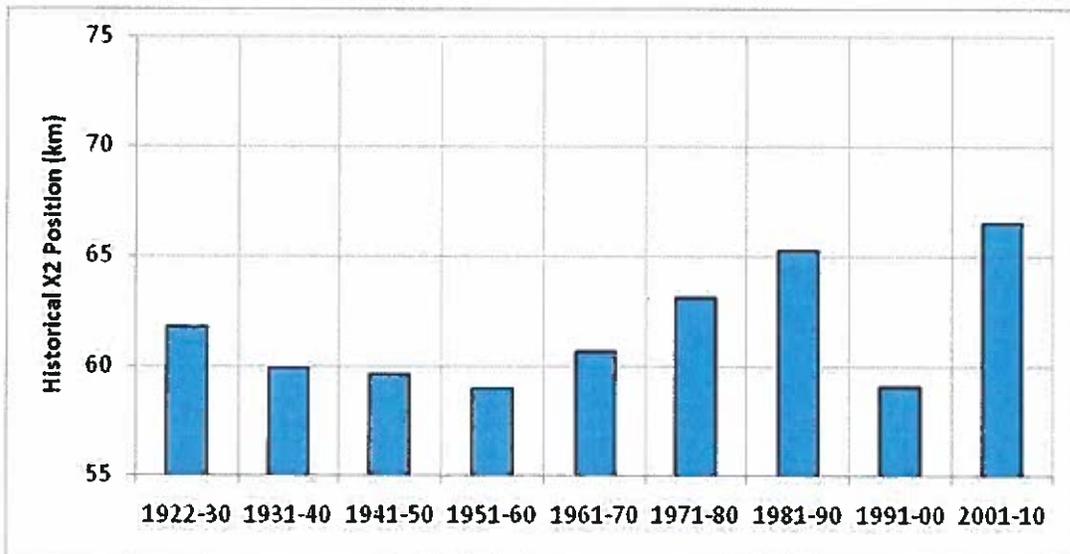


Figure 22 Calculated X2 location in March 1922–2010. The most recent decade (2001–2010) is most comparable to the decade 1981–1990. In the most recent decade (2001–2010) X2 was further upstream on average than in the prior decade (1991–2000).



Figures 16 through 22 show that the calculated X2 has been greater each month (January -June) in the decade 2001–2010 than it was in the prior decade 1991–2000. To understand the reason for this difference in the X2 location, Figures 23 and 24 compare changes in inflows and water diversions between the decades 1991–2000 and 2001–2010. These figures show that the increase in X2 is due primarily to dryer hydrology. As hydrologic and diversion patterns are different in winter compared to spring, the changes are identified by season winter (January - March) and spring (April-June).

Figure 23 identifies the hydrologic factors that drive the decrease in winter (January-March) outflow from the prior decade (1991–2000) to the most recent decade (2001–2010). The vertical bar chart inset in the top right-hand corner of the figure demonstrates that the difference in outflow is explained in large part by the difference in unimpaired outflow (*i.e.*, the reduction in unimpaired outflow [red bar at 6,273 TAF/year] accounts for the majority of the reduction in outflow (blue bar at 6,745 TAF/year)). Thus, the outflow reduction between decades is primarily the result of dryer hydrologic conditions. Water management also contributed to the outflow reduction. The horizontal blue bars in the main body of the figure represent normalized contributions by individual hydrologic drivers towards the decrease in annual outflow between decades. These horizontal blue bars sum to the difference between the vertical bars. The horizontal blue bars in the main body of the document represent changes in outflow other than hydrology. The figure shows that, after reduction in unimpaired outflow, CVP/SWP operation (434 TAF/year) is the next most significant hydrologic factor in explaining the decrease in winter outflow between the 2 decades. In other words, Figure 23 shows that 93% of the outflow difference (6273 TAF v. 6745 TAF) is due to changes in unimpaired flow (drier hydrologic conditions) and that CVP/SWP operations comprise only 6% of the difference (434 TAF v. 6745 TAF).

Figure 23 Contribution to decrease in January- March Delta outflow (1991–2000 compared to 2001–2010). Changes in unimpaired flow (drier hydrologic conditions) explain 93% of the difference in outflow between these decades. CVP/SWP operations explain only 6% of the difference.

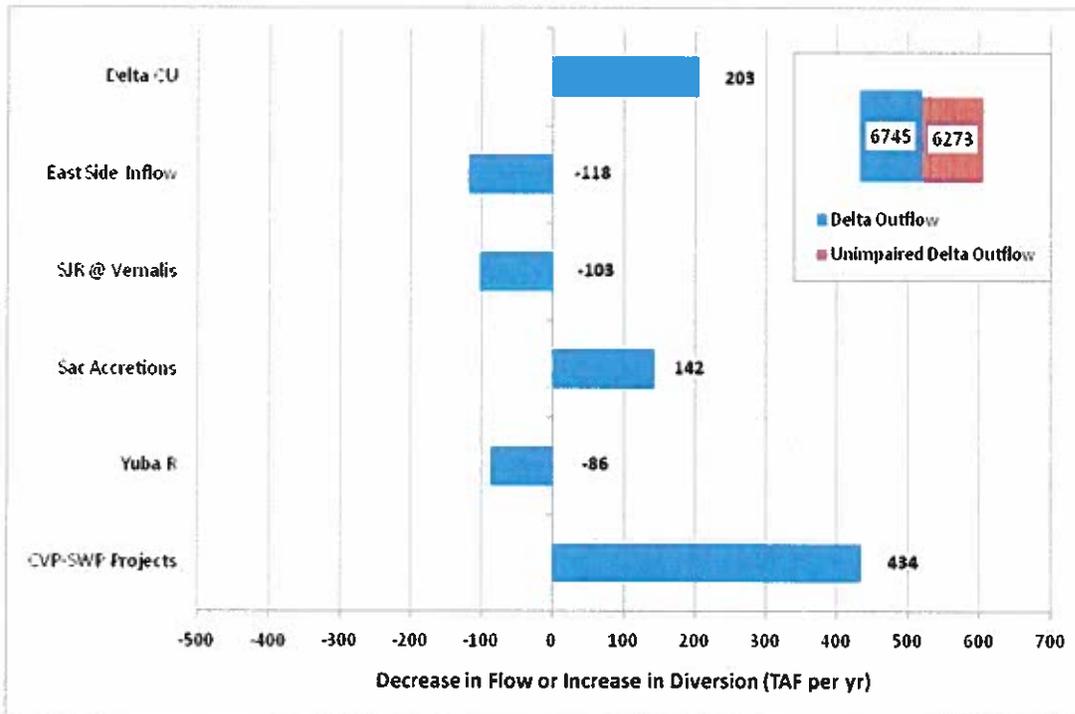
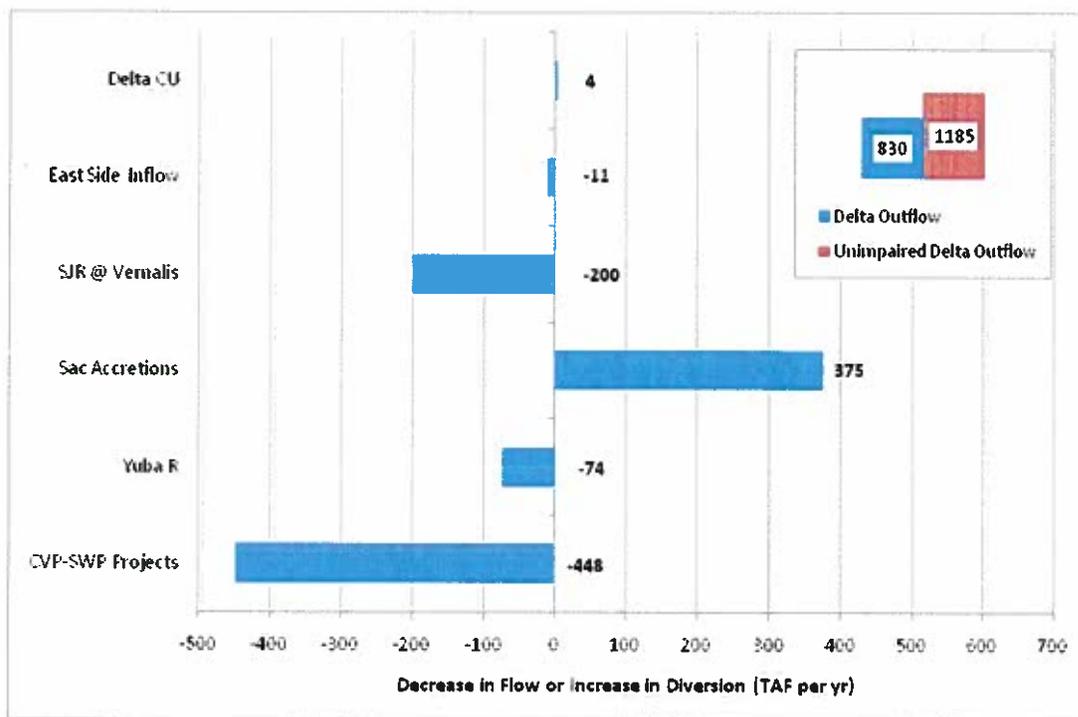


Figure 24 identifies the hydrologic factors that drive the decrease in spring (April-June) outflow from the prior decade (1991–2000) to the most recent decade (2001–2010). The vertical bar chart inset in the top right-hand corner of the figure demonstrates that the difference in outflow is less than is explained by the difference in unimpaired outflow (*i.e.*, the reduction in unimpaired

outflow [red bar at 1,185 TAF/year] is larger than the reduction in outflow [blue bar at 830 TAF/year]). In other words, drier hydrologic conditions can explain all of the reduction in outflow between decades. The horizontal blue bars in the main body of the figure represent normalized contributions by individual hydrologic drivers towards the decrease in annual outflow between decades. These horizontal blue bars sum to the difference between the vertical bars. The horizontal blue bars in the main body of the document represent changes in outflow other than hydrology. The figure shows that, after reduction in unimpaired outflow, reduction in Sacramento Valley accretions (375 TAF/year) is the next most significant hydrologic factor contributing to decrease in winter outflow between the 2 decades. The CVP-SWP Projects (-448 TAF/year) and San Joaquin River flows at Vernalis (-200 TAF/year) actually contributed to higher outflow.

Figure 24 Contribution to decrease in April-June Delta outflow (1991–2000 compared to 2001–2010). The difference in outflow between the decades is less than the difference in unimpaired outflow; therefore drier hydrologic conditions can explain all of the reduction in outflow. The CVP/SWP Projects and San Joaquin River flows at Vernalis actually contributed to higher outflow.



3.1.6 Calculation of predevelopment outflow

In the 2010 Flow Criteria Report, and in presentations by certain stakeholders in the ongoing Delta Plan review workshops, a percent of the unimpaired hydrograph approach has been proposed as a method of regulating future Delta inflows and outflow. The fundamental assumption underlying the percent of the unimpaired hydrograph approach is that the unimpaired flow is a valid or otherwise useful estimator of predevelopment or “natural” flows. It is not. The term “unimpaired” outflow leads many to wrongly believe it means “natural” or pristine.

Unimpaired inflows is a calculation intended to represent flow entering the Delta through existing leveed river channels absent storage operations and downstream uses. These flows are assumed to be routed through the existing system of channels and bypasses into the Delta and the Bay, without any losses or modifications on the way and with no recognition of the natural interaction of water with the land, the original incubator of native species (DWR, 2007).

If restoring a more “natural” flow patterns is the goal, regulations based on unimpaired outflow are not going to be effective. The obvious question therefore is what is a valid approach to estimate natural or predevelopment outflow? The Public Water Agencies have been considering that question. They have explored ways to estimate the variability in natural flow, and those next step modeling efforts are described below.

3.1.6.1 Natural flows

The physical structures of the historic Delta (land covers and channel configurations) were very different than exist today. As the physical aspects of the Delta changed over time, local hydrodynamics, hydraulics and flow changed as well. In large portions of the existing Delta, the land and the water are disconnected from each other by levees, native vegetation has been replaced by agriculture, and the once meandering rivers have been channelized. Any estimate of natural flows, including outflows, must account for the fact that the physical environment was dramatically different under natural conditions because those historic structures heavily influenced outflow patterns.

Under natural conditions, the Central Valley functioned as a series of side-stream reservoirs, located alongside the major streams, rather than at the headwaters of the streams. These stream-side reservoirs filled and drained every year. Thus, the natural rim inflows did not flow unimpeded through river channels into the Delta and the Bay. Rather, they spilled over elevated natural levees into side-stream reservoirs, where they were retained, diminished and ultimately returned to the channel.

Under natural conditions, the channels of the major rivers were not adequate to carry normal winter rainfall runoff and spring snowmelt (Grunsky, 1929). They overflowed their banks into vast natural flood basins flanking both sides of the Sacramento and San Joaquin Rivers (Hall, 1880). Water flowed over the levees in thin sheets, until the water level on the non-river side of the levees rose and joined with the water surface in the channel. When this happened, all visible trace of a channel was lost and the area took on the appearance of a large inland sea (Grunsky, 1929, p. 796). In the San Joaquin Valley in July 1853, for example, engineers surveying a route for a railroad, reported:

The river [San Joaquin] had overflowed its banks, and the valley was one vast sheet of water, from 25 to 30 miles broad, and approaching within four to five miles of the hills.

(Williamson, 1853, p. 12). The filling and emptying of these flood basins had the effect of delaying the transmission of flood flows down the major rivers, reducing peak flows and velocities (TBI, sec. IV.B.1 and Grunsky, 1929). Some of the water in these flood basins gradually drained back into the main river channels after the floods subsided, through a complex

network of sloughs. Some basins drained relatively rapidly while others retained flood waters through the summer or year round (Grunsky, 1929, p. 793 and 796; McGowan, 1961; Thompson, 1961, Olmstead and Davis, 1961, pp. 25-27). These flood basins also contained vast tracts of tule marsh, which retarded the drainage of the basins and evapotranspired residual flood waters (Babtist *et al.*, 2007). The resulting delayed transmission and reduced volume of flood and other natural flows is not reflected in unimpaired flows. Thus, setting monthly flow standards based on a percentage of monthly unimpaired flows is not relevant to the original landscape that nurtured the species the State Water Board seeks to protect.

The main river channels were lined by wide levees that were built up over time from sediment deposited as rivers spread out over the floodplain. These levees were much larger and more developed along the Sacramento River than along the San Joaquin River (Hall, 1880, part II, p. 51). Along the Sacramento, the natural levees rose from 5 to 20 feet above the flood basins and ranged in overall width from about 1 to 10 miles, averaging 3 miles (Thompson, 1961, p. 297). The southern reaches of the San Joaquin River developed natural levees only poorly due to low sediment loads (Hall, 1880, part II, p. 51), and only as the river entered the valley floor (Warner and Hendrix, 1985, pp. 5.15-5.16), sustaining large freshwater marshes still found there today (Katibah, 1984 and Garone, 2011, p. 79). However, natural levees did form along the major northern San Joaquin River tributaries -- the Tuolumne, Stanislaus, Merced, Mokelumne, Cosumnes, and northern San Joaquin (Warner and Hendrix, 1985, p. 5.15). Lush riparian forests occupied these levees.

The flood basins also received flow from sources other than flood flows spilling over the natural levees. These included upland runoff and west- and east-side streams, e.g., Stony, Cache, Putah. These were blocked from reaching the main river channels by the natural levees. They spread out over the valley floor, pooling in expansive sinks of tule marsh and connecting to the main rivers only by subsurface flow (Garone, 2011, p. 23; Thompson, 1961, p. 299). Further, breaches or “crevasses” in the natural levees and percolation of water through the relatively coarse, porous levees permitted excess waters to escape the main streams and spread over the low flood plains (Thompson, 1960, pp. 352-353).

This highly productive system was completely replumbed to control floods, facilitate the irrigation of the valley, and for navigation. The channels were dredged and rip-rapped, the levees were raised, the flood basins were drained, bypasses installed, and head-stream reservoirs were built to replace the side-stream storage and generate electricity.

The Sacramento and San Joaquin Rivers discharged into the Delta, which is a product of its topography. As the rivers descended from the mountains toward sea level near their confluence, their gradients decrease dramatically, reducing their velocity and ability to incise their channels. Thus, they distributed their flow into numerous sloughs that meandered across the landscape (Garone, 2011, p. 27) to a common mouth into Suisun Bay. Shoals were present at the mouth of the rivers, one notably opposite Collinsville, which was an obstruction to the escape of flood waters from the Sacramento River (Hall, 1880, part II, p. 23). An appreciable amount of Sacramento River water below Sacramento was originally (and continues to be) routed through the Georgiana and Three-Mile sloughs into the San Joaquin River (Hall, 1880, p. 47).

Under natural conditions, these rivers were braided together in the Delta in a complex arrangement of channels weaving through flat, low-lying islands with elevations at or below sea level. These islands were submerged for much of the year, with water levels fluctuating with the tides and river flood stages. The islands' outer margins had small natural levees while the interior sections were marsh. When river flows were high in spring, the historical Delta was a morass of flooded island and marshes. In late summer, when river flows were low, the islands and marshes, protected by low natural levees, were often surrounded by saline water pushed upstream by tides. Nearly 50% of the Delta was originally submerged by daily tides (Thompson 1957, p. 21; Thompson 1961, p. 299). Dominant vegetation in the saucer-shaped islands included tules and on higher levee ground, coarse grasses, alder, walnut, and cottonwood (Thompson, 1957, chapters 1-2, pp.135-136; Thompson, 1961, p. 299; Hall 1880, part II, Moyle, 2002, p. 32). By the 1930s, these vast areas of Delta tidal wetlands and riparian vegetation were diked, drained, and converted into islands of farmland surrounded by high levees, now highly subsided; the sloughs were replumbed and deepened; and sand bars were removed, completely altering the natural hydrodynamics and its rich and diverse habitat for native species (Thompson, 1957, Lund *et al.*, 2010, Ch. 2, 3, and 5).

Finally, under natural conditions, groundwater moved generally from recharge areas along the sides of the valley towards topographically lower areas in the central part of the valley, where it discharged primarily as evapotranspiration from marshes and riparian forests (TBI, Sec. IV.B.2; Bertoldi *et al.*, 1991, pp. A17, A23, Fig. 14A; Williams, 1989, p. D33; Davis, 1959, p. 86). Groundwater was near the surface in much of the Valley (Bryan, 1915, p. 19 and plate 11; Kooser *et al.*, 1961, pp. 265 and 278). The U. S. Geological Survey estimated that under natural conditions, the groundwater table was less than 10 feet below the surface over about 62% or 8,000 square miles of the Central Valley (Williamson *et al.*, 1989, P. D40). The groundwater system was in a state of dynamic equilibrium. Natural recharge was balanced by natural discharge. This has been recently confirmed for the San Joaquin Valley (excluding the Tulare Basin) using a physically based, surface-subsurface numerical model (HydroGeoSphere) (Bolger *et al.*, 2011, pp. 322-330). The natural groundwater system has been extensively altered by pumping for irrigation and other uses, resulting in widespread overdraft and land subsidence.

3.1.6.2 Estimation of pre-development land cover

There is general agreement within the scientific community regarding the nature of the physical environment that existed in the pre-development era. A recent San Francisco Estuary Institute ("SFEI") study further collaborates the natural flow description provided above (see SFEI Report at http://www.sfei.org/news_items/press-delta-historical-ecology-report). However, there is yet to be general agreement on how many acres of each land cover type existed and the land cover's cumulative consumptive water use.

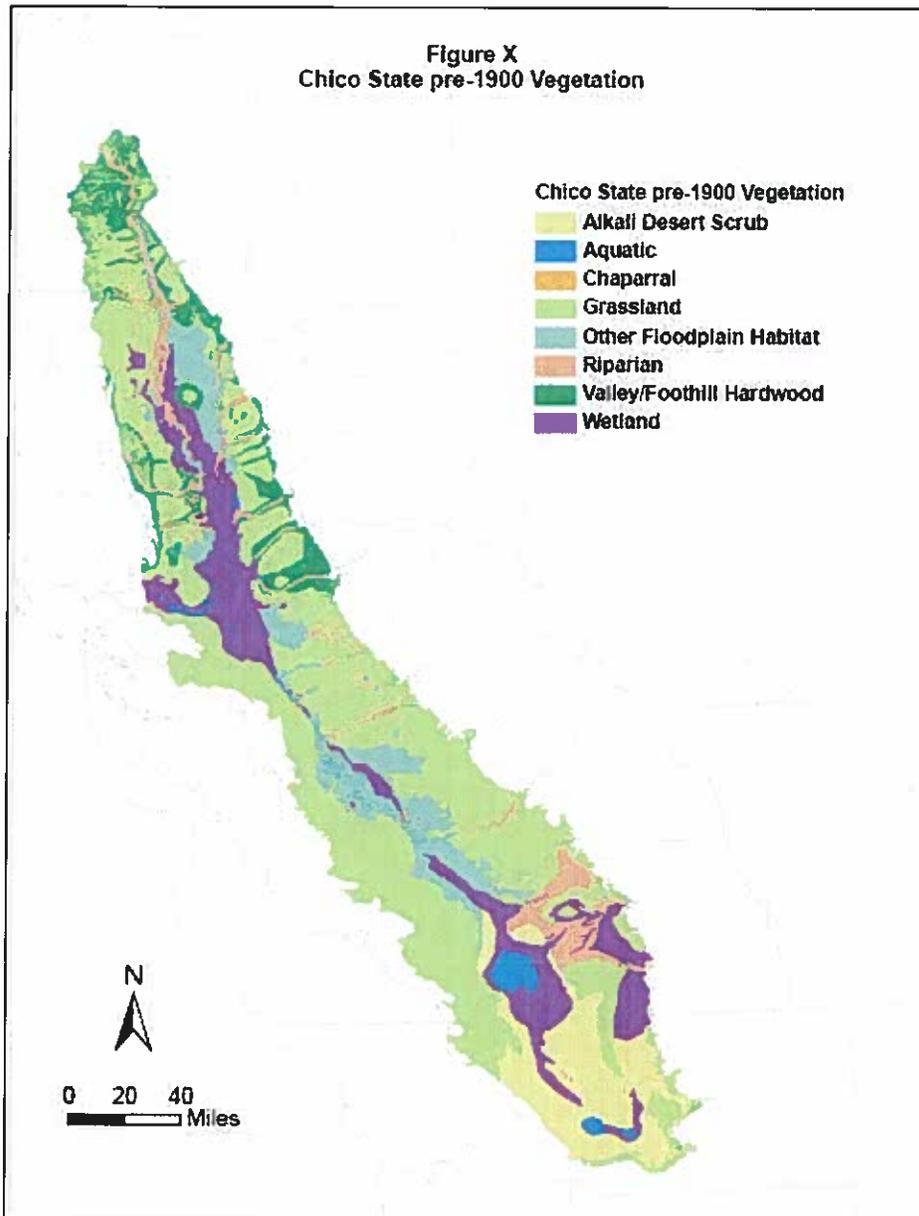
In 2003, California State University-Chico ("Chico") completed a historic mapping effort to determine the acreages of the various types of native vegetation that once covered the Delta and its watershed. The Chico effort mapped four different time periods, with the "pre-1900" map being of particular interest for purposes of calculating predevelopment (pre-1900) outflow.⁴ To

⁴ Chico (2003) has been referenced in at least two published works: Bolger et al. 2011 and Barbour *et al.* 2007.

create its maps, Chico reviewed and digitized approximately 700 historic maps, searching numerous collections of historic maps in public libraries. For this report, Dr. Phyllis Fox confirmed the accuracy of the Chico State pre-1900 map using several sources, including: Hall (1887); Küchler (1977); Roberts *et al.* (1977); Dutzi (1978); and Fox (1987). These archival maps and others were scanned (400-dpi full color scanner), the scanned versions were georeferenced⁵ using various data layers (e.g., county, township), and the map features were digitized by hand using editing features in ArcMap. ArcMap's geoprocessing tools were used to determine areas of the various types of vegetation.

⁵ Transforming scanned images into maps with reference coordinates.

Figure 25 Chico (2003) pre-1900 map.

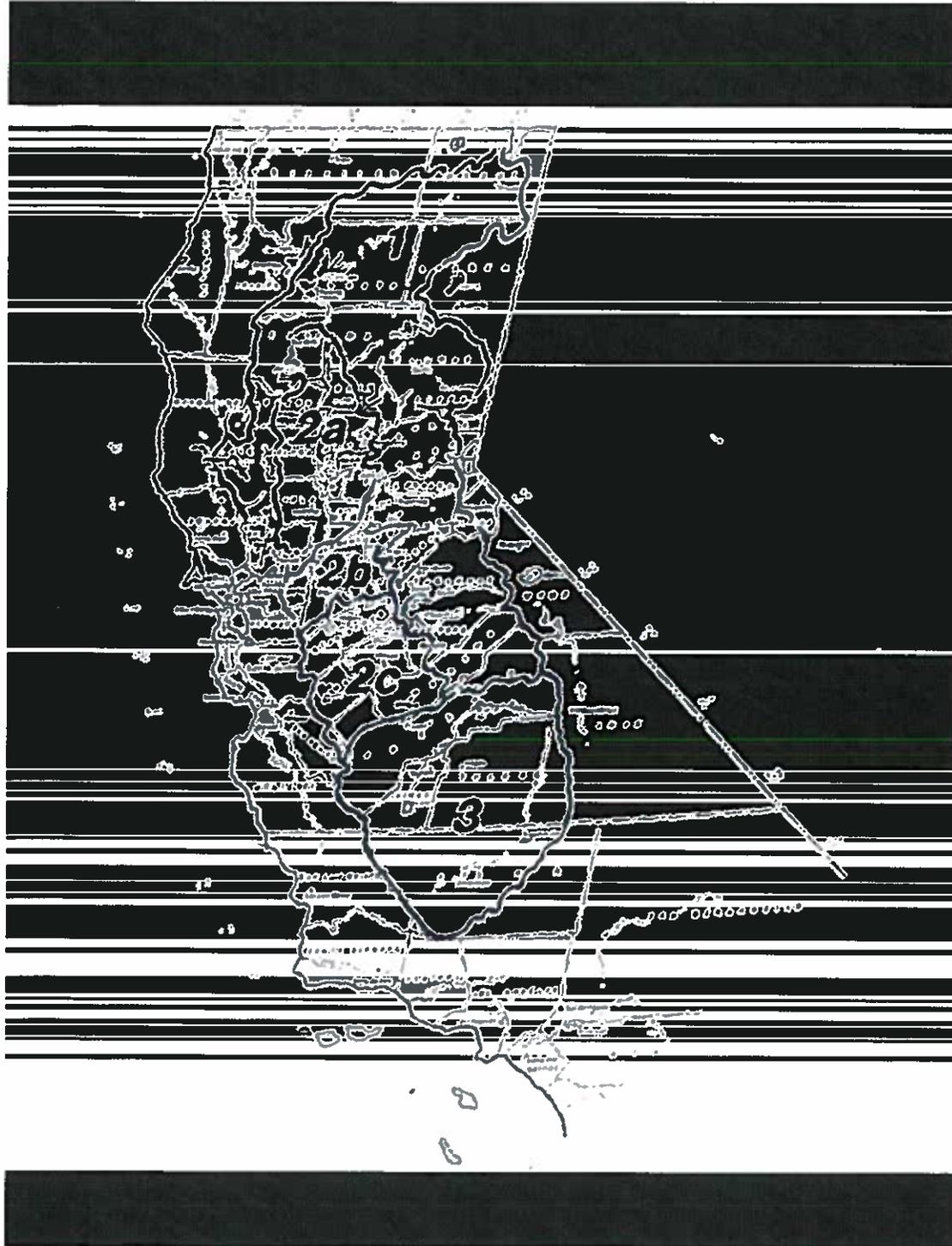


Chico (2003) estimated land cover throughout the Central Valley. We divided the area that drains into the Bay into upper, middle and lower region to correspond with DWR's hydrologic units, as defined by DWR in California Central Valley Unimpaired Flow Data, Second Edition, February 1987.⁶ The DWR drainage area encompasses the Sacramento Valley (Area 2a), the Delta and upslope areas (Area 2b), and the San Joaquin Valley Area (Area 2c). These three

⁶ DWR has updated its designation of basins and boundaries since the 2nd edition, and future estimates will reflect that new information.

areas define the rim of the valley where the unimpaired flows are gauged. See Figure 26, DWR hydrologic units.

Figure 26 Hydrologic Units Used in Calculating Freshwater Inflow to San Francisco Bay Under Natural Conditions, DWR 1987.



We estimated acreages of each type of vegetation by drainage basin based on Chico pre-1900 map using ArcMap’s “Calculate Geometry” feature. The results of this analysis, by drainage basin, are summarized in Table 2 discussed below for each vegetation type.⁷

Table 2 Natural Vegetation Land Area (acres), Chico (2003)

	Sacramento Basin (2a)	Delta (2b)	San Joaquin Basin (2c)	Totals
Vegetation	(Acres)	(Acres)	(Acres)	(Acres)
Aquatic	32,616	18,319	9,242	60,177
Grassland	1,591,415	615,799	2,263,714	4,470,928
Other Flood Plain Habitat	474,743	117,101	572,291	1,164,135
Riparian	443,852	54,930	72,192	570,974
Valley/Foothill Hardwood	639,650	197,656	9,268	846,574
Wetland	529,814	395,354	86,497	1,011,665
Total	3,712,090	1,399,159	3,013,204	8,124,453

It is unknown if Chico’s estimates accurately depict “pre-development” conditions as significant modifications to the physical environment and large scale farming had already begun by the turn of the 20th century. The earliest resource map used by Chico is 1874 (Chico, 2003, Table 1). To the extent Chico’s estimates reflect early development, Chico underestimates natural land cover, and as a result, underestimates natural evapotranspiration.

There is some uncertainty regarding Chico’s land cover estimates, primarily because of the various assumptions associated with using numerous archival resources, with varying degrees of accuracy, that cover a range of years. Nevertheless, it appears that the Chico estimates are consistent with findings of other similar research efforts, as discussed below.

3.1.6.2.1 Description of historic grasslands

The plains were smooth and nearly level lands that were formed as flood waters spread over them, leaving behind thick deposits of silt. The vegetation in the grasslands was prairie, as variously defined by Heady (1988), Küchler (1977), and Bartolome et al (2007). The original grassland no longer exists. What it once looked like and contained can never be known with certainty as early eye witness accounts are vague. The best guess by experts is that it was dominated by two species of needlegrass (*Stipa cernua* and *S. pulchra*).

Vernal pools (or “hog wallows”) were present within the grasslands but were not separately mapped by Chico. These are seasonal ephemeral wetlands that fill and dry out each year. They

⁷ “Chaparral” was removed from the land cover estimates as it was insignificant, totaling a few hundred acres.

are shallow depressions underlain with an impermeable layer of soil. In winter, the hardpan soils underlying these pools prevent water from penetrating, saturating the upper soil and filling the basin with water, thus forming pools and small lakes. Rainfall collects in the depression, stands through early spring, then evaporates as temperatures rise and rainfall declines. The soil remains moist through April and May and then desiccates (Solomeshch, 2007). However, this does not imply they do not contribute to water losses.

The Central Valley vernal pools appear to be supported by perched aquifers. Seasonal surface water and perched groundwater connect uplands, vernal pools and streams (Rain *et al.*, 2006). Thus, these aquifers may contribute significantly to evapotranspiration. These vernal pools have not been mapped and evapotranspiration from this vegetation type has been treated by Chico (2003) as standard grassland, a likely underestimate.

Most vernal pools are densely vegetated seasonally, primarily with native annual grasses, forbs, and pool-bed algae. They support a rich variety of plants including annual forbs, grasses, rushes, and succulents; cryptophytic perennial herbs, perennial grass and forb halophytes, perennial rushes, cryptophytic perennial forbs, and small shrubs (Solomeshch *et al.*, 2007, p. 398). Rings of vegetation form as the rainfall stops and temperatures rise in late spring. These vernal pools were present throughout the Central Valley under natural conditions, but were most abundant in Fresno, Madera, Merced, Placer, Sacramento, Tehama, and Yuba counties (Solomeshch *et al.*, 2007, p. 398). Most pools are less than 0.02 acres (100 m²) in area, but a few covered tens of acres up to 300 acres and were temporary lakes (Solomeshch *et al.* 2007, p. 398; Barbour *et al.*, p. 83). Under natural conditions, vernal pools may have covered 1 percent of the State's area (Barbour *et al.*, pp. 81-83; Crampton, 1974, p. 30), but they were not separately mapped by Chico.

3.1.6.2.2 Description of wetlands

Chico (2003) described its wetland category as, "Wetland (perennial) – Also considered Freshwater Marsh." Wetlands are among the most productive wildlife habitats in California. They occur on virtually all exposures and slopes provided the depression or basin is periodically flooded. Characteristic species include various species of Cattails (*Typha spp.*), Bullrushes or Tules (*Scirpus spp.*), Rushes (*Juncus spp.*), and Sedges (*Carex spp.*).

The Chico map describes about 1 million acres of perennial wetland. This estimate is confirmed by a number of primary sources, including the federal surveys done pursuant to the Arkansas Swamp Act of 1850, comparable California surveys, independent surveys by the California State Engineer, and technical summaries based upon surveys. One of the most significant of these reports confirming the extent of the tule marshes was prepared by Professor Hilgard, generally regarded as the father of modern soil science and the first director of the Agricultural Experiment Station at the University of California, Berkeley. His report was prepared for the 1880 U.S. Census. It separately listed the area of tule lands in each county, showing a total of 1.2 million acres tributary to the Bay. Another authoritative source, Marsden Manson, assistant to California's first State Engineer, published an estimate of about 1.0 million acres tributary to the Bay in a refereed and archival journal, based on State Engineer surveys. Thus, the value returned by the Chico pre-1900 map is consistent with historical surveys.

3.1.6.2.3 Description of floodplain habitat

This is the second largest category of native land areas, comprising 1.2 million acres, or slightly more than perennial wetlands. “Other Floodplain Habitat” is a category used by Chico to designate areas that are a mixture of wetlands, grasslands, and riparian forest that have not been previously differentiated on historic maps. Our analysis indicates some of the area classified by Chico as “other floodplain habitat” was classified by Dutzi as oak woodlands and savanna. Further, a comparison of the Chico pre-1900 map with early maps based on surveys indicates that much of this land has been mapped as tule marsh by others.

3.1.6.2.4 Description of valley/ foothill hardwood

In the Central Valley, “valley/foothill hardwood” vegetation as mapped by Chico primarily consists of three hardwood areas dominated by oaks: (1) the open woodland around the rim of the Central Valley; (2) savannas with trees widely spaced and scattered over grasslands, and (3) the densely wooded, thickly canopied oak riparian areas on the upper edge of levees along rivers (valley oak riparian forest) (Barbour and Major, 1988, pp. 387-405, 425-55; Allen-Diaz *et al.* 2007; Shelton 1987; Dutzi 1978; Pavlik *et al.* 1991, p. 9 and 63-64; Anderson 2006, pp. 30-32). The divisions between these three categories are somewhat arbitrary; gradations of communities exist between the savanna and riparian types.

The Chico map returned 847,000 acres of this vegetation type in the study area. Of this, 640,000 acres was in the Sacramento basin (basin 2a); 198,000 acres in the Delta (basin 2b); and 9,000 acres in the San Joaquin basin (basin 2c). This estimate is within the range of estimates by others. Shelton (1987) estimated 494,000 acres of “valley oak savanna,” a subset of valley/foothill hardwood area mapped by Chico, reporting none in either the Delta or San Joaquin. Dutzi (1978) estimated 1.5 million acres of “valley oak woodland and savanna” in the Sacramento Valley, which includes all three categories mapped by Chico.

3.1.6.2.5 Description of riparian

Riparian vegetation was found along all of the low-velocity waterways in the Central Valley, but the largest areas occurred on the rivers with the largest natural levees. The riparian forest extended from the banks to the edge of the moist soil zone, and, in many cases, as far as the hundred-year flood line, up to 4 to 5 miles on each side on the lower Sacramento River, where natural levees were widest (Garone 2011, pp. 24-25; Katibah 1984, p. 24). They were also present along tributaries of the main rivers and the upper San Joaquin River (Roberts *et al.* 1977, Figure 2; Warner and Hendrix 1985, pp. 5.10 - 5.11; Williamson 1853, p. 12).

The Chico map describes 571,000 acres, of which 444,000 acres are in the Sacramento Valley (basin 2a); 55,000 in the Delta (basin 5b); and 72,000 acres in the San Joaquin Valley (basin 2c). Chico’s estimate for the Sacramento Valley (444,000 acres) is about equal to Dutzi’s (1979) estimate for this area (438,000 acres), which is not surprising as Chico relied on Dutzi for its pre-1900 mapping. The difference is primarily due to differences in the boundary of the Sacramento Valley.

However, Chico's estimate for the study area (571,000 acres) is low compared to estimates by others including K uchler 1977 (874,000)⁸; Roberts *et al.* 1977 (937,900 acres)⁹; Katibah 1984 (921,000 acres); and Warner and Hendrix (1985). Warner and Hendrix comprehensively reviewed estimates available through 1985 and concluded that "the present 'best estimate' of pre-settlement riparian wetlands vegetation in the Central Valley is at least 1,600,000 acres...". Chico mapped areas shown by others as riparian forest as grasslands or other floodplain habitat, which use less water. Further, Chico separated out the riparian oak fringe of the riparian zone in some areas, which is generally included in most estimates of riparian acreage. Barbour *et al.* (1993), for example, estimated 900,000 acres of riparian forest, which they described as including the fourth zone, or the valley oak forest (Barbour *et al.* 1993, pp. 74-75).

3.1.6.2.6 Description of aquatic

Chico defined "aquatic" as including major water bodies, including lakes, reservoirs, and estuaries. Under natural conditions, the Central Valley contained open water surfaces, including lakes, sloughs, and overflow basins. The open water surface area was determined from historic sources to be about 68,000 acres (SWC, 1979). This compares favorably with the Chico (2003) estimate of aquatic areas of 60,000 acres. Water surface evaporation was calculated using the historic area and annual average pan evaporation data (5.6 ft/yr). The pan data was measured at Gerber. It was supplied by DWR and is used in their CalSim 3.0 model (Cheng, 2012).

3.1.6.3 Estimation of evapotranspiration of natural vegetation

To estimate consumptive use of native vegetation in the pre-development era, the evapotranspiration ("ET") rate (acre-feet per year) for each vegetation type must be identified and calculated (acre-feet per year).

ET is the sum of water lost by evaporation from the soil and open water surface plus loss from interception by vegetative cover and transpiration from plants. Transpiration is the loss of water from plants in the form of vapor that occurs primarily through stomates, microscopic holes in the leaves through which water is lost and carbon dioxide enters for growth. Lesser amounts are lost through the cuticle and lenticels in the bark (Kramer and Boyer, 1995). A leaf that facilitates the uptake of carbon dioxide (CO₂) and thus growth is also favorable for the loss of water. Thus, transpiration is related to canopy size, plant size, density, leaf area, etc. (Cowan, 1982, pp. 535-562; Devitt *et al.* 1994, pp. 452-457). These are important considerations here as the native vegetation was consistently described in eye witness accounts as large, immense, and lush. The evaporation component, on the other hand, is controlled by climatic conditions.

Generally, there are several methods to determine evapotranspiration. These include lysimeters, soil water balance, bowen ratio, eddy covariance, remote sensing energy balance, and sap flow measurements, among others. All of these methods contain degrees of error. We have used two methods in this report to estimate the ET rate of native vegetation: literature review of field

⁸ As reported by Shelton 1987.

⁹ The Roberts *et al.* 1977 map was digitized and the area determined using the "Calculate Geometry" feature in ArcMap returning 638,451 acres in the Sacramento Valley (basin 2a), 131,931 acres in the Delta (basin 2b), and 114,862 acres in the San Joaquin Valley (basin 2c).

experiments and climate based assessment calculations. This analysis provides preliminary estimates based on both methods.

3.1.6.3.1 Results of evapotranspiration field experiment literature review

Research on the rate of vegetative evapotranspiration has been going on for decades. The calculated ET values from the literature review provided in Table 10 are used as comparison against the values measured by researchers. The reasons for providing a comparative range is that the science of measuring ET is evolving and many of the published field studies were conducted in locations outside of the Central Valley so the actual vegetation evapotranspiration (ET_c) values may not be accurately represent the pre-development conditions in the Central Valley. However, the purpose of this literature review is to show the variable magnitude of field study measurements.¹⁰ Results of this literature review are presented in Tables 3 through 5, below.

Table 3 Water Use by Tules and Cattails

Locations	Type of Marsh	Annual Water Use (ft/yr) ^d	Reference
King Island, Delta	Freshwater tidal marsh	7.4 – 13.0 ^a	Stout (1929-35)
Victorville, CA (Mojave River)	Desert inland marsh	6.5 – 7.0	Young and Blaney (1942)
Mesilla Valley, NM (Rio Grande River)	Freshwater marsh	10.1	Young and Blaney (1942)
Bonner’s Ferry, ID	Inland marsh	5.1	Robinson (1952)
Antioch, Delta	Freshwater tidal marsh	5.8 ^b	Blaney and Muckel (1955)
Clarksburg, Delta	Freshwater tidal marsh	9.6 ^c	DPW (1931b)

- a. Value for third year of growth. Range corresponds to two different tank configurations.
- b. Calculated based on limited experiments at Joice Island in Suisun Marsh.
- c. Experiments conducted in isolated tanks and values adjusted by multiplying by a factor of about 0.5.
- d. All values measured in tank experiments in which tanks were set in natural environment unless otherwise stated.

¹⁰ As some early ET studies had various methodical limitations, the American Society of Civil Engineers (ASCE) convened a task force to review the early literature. The 1989 ASCE report identified certain studies as “outstanding research” and contains a complete bibliography of ET studies widely considered reliable. Many of the citations presented herein were characterized by the ASCE as “outstanding,” particularly those conducted by Blaney and Young in the Delta and elsewhere in California.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

Table 4 Water Use by Native Grassland Vegetation

Vegetation	Annual Water Use (ft/yr)	Location	Reference
Field Studies			
Native brush	1.4 – 1.8	San Bernadino, CA	Young and Blaney (1942)
Native brush	1.5	Muscoy, CA	Young and Blaney (1942)
Native brush	1.2	Claremont, CA	Young and Blaney (1942)
Native brush	1.6	Palmer Canyon, CA	Young and Blaney (1942)
Native grass and weeds	0.8	San Bernadino, CA	Young and Blaney (1942)
Native grass and weeds	1.1-1.25	Cucamonga, CA	Young and Blaney (1942)
Native grass and weeds	1.0	Anaheim , CA	Young and Blaney (1942)
Native grass and weeds	1.1	Ontario, CA	Young and Blaney (1942)
Native grass and weeds	1.1	Wineville, CA	Young and Blaney (1942)
Annual grasses, forbes, and legumes	1.2	Placer County, CA	Lewis (1968)
Grasslands	0.8-1.3 (7/01-6/07)	Lower Sierra Nevada Foothills, Vaira Ranch	Ryu et al (2008) Baldocchi et al. 2004
Tank Studies			
Annual grasses	0.8 - 1.2	Placer County, CA	Lewis (1968)
Grass	1.2	San Luis Rey, CA	Blaney (1957)
Grasslands	0.9 – 2.9	Sierra Ancha, AZ	Rich(1951)
Grasses	2.2	Sierra Ancha, AZ	Rich (1951)

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

Table 5 Water Use by Common Riparian Vegetation

Vegetation	Annual Water Use (ft/yr)	Location	Reference
Field Studies			
Canyon-bottom, Lower Reach: 82% alder, 8% sycamore, 4% Bay, 3% willow, some maple, oak. Understory grapevine & blackberry.	6.9 ^a	Coldwater Canyon, CA	Blaney (1933)
Canyon-Bottom, Upper Reach: 48% alder, 26% Bay, 9% maple, 7% willow, 6% sycamore, some oak, cedar, spruce, etc. Same understory.	5.4 ^a	Coldwater Canyon, CA	Blaney (1933)
Moist-land vegetation, including willows, tules and other unspecified vegetation	9.5 ^b	Temescal Canyon, CA	Blaney et al. (1933)
River-bottom brush comprising 38% heavy tree cover of willows, alders, cottonwood, sycamore; 19% grass, 20% brush, 6% tule swamp	4.2	Santa Ana River, CA	Troxell (1933)
Tank Studies			
Isolated clump of 7 ft tall red willows	4.4	Santa Ana, CA	Blaney et al. (1933)
Mixture of cottonwoods and willows	5.2 – 7.6 ^c	San Luis Rey, CA	Blaney (1957, 1961)
Alders	5.0	Santa Ana, CA	Muckel (1966)
Cottonwoods and willows	7.6, 6.0 ^c	Safford Valley, AZ	Gatewood et al. (1950)

- a. Reported for the 4-month period May-October 1932 and converted to a 12-month basis using the monthly distribution of water use for willows, by dividing 0.77 [DPW 1931b].
- b. Reported for the month of May 1929 and converted to a 12-month basis using the monthly distribution of water use for willows by dividing by 0.11 [DPW 1931b].
- c. Range depends on depth to groundwater, which varied from 3 to 4 feet at San Luis Rey and 7 ft at Safford Valley. Varies reported as 7.6 ft/yr in Table 29 for cottonwood and willow and 6.0 ft/yr for cottonwood at 195 and 203.

In the first oak woodland study, Lewis (1968) measured consumptive use for three oak woodland watersheds (12-47 acres) in the Sierra-Nevada Foothills in Placer county. The predominant hardwood was interior live oak (*Quercus wislizenii*) associated with varying amounts of blue oak (*Quercus douglasii*) and black oak (*Quercus morehus*) with some digger pine (*Pinus sabiniana*) and poison oak, annual grasses, legumes and forbes as ground cover. The measure evapotranspiration averaged 1.7 ft/yr and ranged from 1.4 to 2.0 ft/yr over a 10 year period, from 1956-1966.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

In 2000, Lewis et al. published another similar study on another similar watershed, in the Sierra-Nevada Foothills in Yuba County. The woodland was dominated by blue oaks (*Quercus douglasii*) and intermixed with interior live oaks (*Q. wislizenii*) and foothills pine (*Pinus sabiniana*); annual grasses and legumes dominated the ground cover. The 17- year average consumptive use for the period 1981-1997 in the Yuba County study was 1.2 ft/yr, with a range of 0.9 to 1.8 ft/yr.

The results of the initial review of ET field studies are summarized in Table 6 as a range of possible ET_c rates.

Table 6 Summary table, evapotranspiration of native vegetation based on field studies

Land Cover	Minimum ET _c (ft. / yr.)	Maximum ET _c (ft. / yr.)
Riparian Forest	4.2	9.5
Wetland	5.1	13
Grassland	0.8	2.9
Valley/Foothill Hardwood	0.9	4

3.1.6.3.2 Climate based assessment (ET rates)

To provide a comparison on the ET rates measured in published field experiments, Dr. Daniel J. Howes from the Irrigation Training and Research Center (ITRC) at California Polytechnic State University, San Luis Obispo calculated upper limit (or potential) of ET_c rates for Riparian Forest, Wetland, Other Floodplain Habitat, and Open Water. A simplified soil water balance was used to estimate ET_c for Grassland habitat. Dr. Howes' initial ET calculation is as follows:

The potential evapotranspiration rate is limited based on available energy in a natural system and the availability of water to the vegetation. Energy exchange at the vegetative surface governs evapotranspiration and is limited by the amount of available energy (Allen *et al.*, 1998, Allen *et al* 2011). The equation for the energy fluxes of an evaporating surface with a large extensive vegetative surface is $\lambda ET = R_n - G - H$ where:

λET is the latent heat flux (representing evapotranspiration)

R_n is the net radiation

H is the sensible heat flux

G is the soil heat flux.

While the different fluxes can be positive or negative, a positive R_n supplies energy in the form of radiation to the system and positive ET , G , and H remove energy from the system.

A convenient way to examine vegetative water use is to measure local weather parameters and compute a reference evapotranspiration, then to use a vegetation specific coefficient to adjust the reference evapotranspiration to the actual vegetation evapotranspiration. In California, a well watered grass reference surface is used as the basis for the reference evapotranspiration (grass reference evapotranspiration, ET_o). Alfalfa is used as a reference in other parts of the U.S. The actual vegetation evapotranspiration (ET_c) will differ from ET_o depending on available water supply, albedo (reflectance of incoming solar radiation), vegetative cover density, vegetative health, growth stage, aerodynamic properties, and leaf and stomata properties (e.g. canopy resistance) (Allen *et al.* 1998). The coefficient to adjust ET_o to ET_c is termed a crop coefficient in agriculture but the term ET_o Fraction (ET_oF with "o" denoting a grass reference crop) is used here to limit confusion since natural vegetation is being examined not agricultural crops. ET_c can be estimated from ET_o and ET_oF as:

$$ET_c = ET_oF \times ET_o \quad \text{Eq. 1}$$

ET_o is computed based on local weather parameters from a specialized weather station that is specifically located in a setting without obstructions from wind surrounded by healthy, well watered vegetation. ET_o is computed using the 2005 Standardized ASCE Penman-Monteith equation (PM-ET_o) (Allen *et al.*, 2005). Using a clipped grass as the reference, specific known properties of grass, including albedo, aerodynamic resistance, and bulk surface resistance, are used in the PM-ET_o equation.

ET_oF is an adjustment factor based on the vegetation and soil properties to be examined. There are many types of vegetation that have higher potential to evapotranspire water compared to grass, therefore ET_oF can be greater than 1.0. The limitation of available energy means that ET_oF has limitation as well. For natural vegetation, that has sufficient available water, with full ground cover, the maximum ET_oF can be computed as (Allen *et al.*, 1998):

$$ET_{oF_{max}} = ET_{oF_h} + [0.04(u_2 - 2) - 0.004(RH_{min} - 45)] \left(\frac{h}{3}\right)^{0.3} \quad \text{Eq. 2}$$

Where ET_oF_h = 1.0+0.1*h for vegetation heights less than or equal to 2 meters (~6.5 feet) and equal to 1.2 with vegetation heights greater than 2 meters. RH_{min} is the minimum relative humidity during the day, u₂ is the wind speed measured at 2 meter above the ground surface, and h is the vegetation height. Where there is standing water with the vegetation (*i.e.* wetlands), a value of 0.05 is added to the ET_oF_{max} computed with the previous equation to account for additional evaporative losses (Allen *et al.*, 1998).

Daily weather data was obtained from five CIMIS weather station (Durham and Gerber in the Sacramento Valley, Twitchell Island in the Delta, and Modesto and Firebaugh in the San Joaquin Valley) to evaluate the ET_oF_{max} for applicable habitat in the evaluated in the water balance. The ET_oF_{max} values were weighted based on daily ET_o values over the timeframe analyzed which was 25 years for some station to 13 years for another depending on data availability. The ET_oF for the Aquatic category was not computed using the previous equation, instead taken directly from Allen *et al.* (1998) for shallow water bodies, because open water does not have the same properties as vegetation. Descriptions of each type of habitat are discussed above.

Table 7 shows the ET_oF_{max} computed from Eq. 2. These values are in agreement with Allen *et al.* (2011) which states that ET_oF should not exceed 1.3- 1.4 in semi-arid climates.

Table 7 Estimated EToF_{max} based shallow water for aquatic and on Equation 2 for the other categories.

Vegetation	Assumed Maximum Height (ft)	Weighted Annual EToF _{max} *		
		Sacramento Valley	Delta	Northern San Joaquin
Aquatic		1.05	1.05	1.05
Other Flood Plain Habitat	6	1.22	1.26	1.22
Riparian	35	1.27	1.35	1.27
Wetland	25	1.30	1.36	1.30

* The EToF_{max} assumes expansive vegetation. In cases where there are small stands of vegetation surrounded by sparse vegetation or dry land, the EToF can be significantly higher (oasis and close line effects). The Chico State pre-1900 vegetation map shows large expanses of these vegetation types so these values should be reasonable.

Grassland ET is highly dependent on available soil moisture. As will be discussed, in some areas the grasses could have access to groundwater. In many grassland habitats, these grasses will be dependent on rainfall to meet their evapotranspiration demands. An initial analysis was conducted to examine a daily soil water balance of rain fed grasslands in each of the three regions. Weather data including ETo and precipitation was obtained from one CIMIS weather station in each region (Gerber in the Sacramento Valley (2006), Twitchell Island in the Delta (2004), and Modesto in the San Joaquin Valley (2001)). Years were selected which had similar precipitation totals as shown in Table 2. Soil type information was estimated for the grassland habitat using NRCS soils map of California.

For the Sacramento Valley, Delta, and San Joaquin Valley north of Fresno the soils were classified on average as silty loam, loam, and loam, respectively. The San Joaquin Valley generally has sandy to fine sandy loam on the east side of the San Joaquin River, and clay loam on the west side. The available water holding capacity for an “average” soil was used which is based on a loam soil. A conservative root zone depth of 3 feet was assumed. The initial analysis resulted in an estimated annual EToF value for grasslands in the Sacramento, Delta, and San Joaquin of 0.3, 0.25, and 0.21, respectively.

No attempt was made to quantify the EToF_{max} for Valley/Foothill Hardwood habitat. It is expected that the ET_c within this habitat will be between Other Flood Plain Habitat and grasslands.

The ETo values used were obtained for this preliminary evaluation from the California Department of Water Resources ETo Zone Map. ETo Zones 12 and 14 are within the Sacramento Valley, Zone 14 covers the Delta, and Zones 12, 14, and 15 cover the San Joaquin Valley north of Fresno. The following table shows the long-term average ETo, precipitation, EToF_{max}, and the maximum likely ET_c for each vegetative habitat within each region.

Table 8 Estimated upper crop evapotranspiration (ETc)

Sacramento Basin Vegetation	Long-Term Average ET _o	Precipitation	ET _o F _{max}	Upper Est. ET _c
	ft/yr			ft/yr
Aquatic	4.6	1.8	1.05	4.8
Grassland	4.6	1.8	0.3	1.4
Other Flood Plain Habitat	4.6	1.8	1.22	5.6
Riparian	4.6	1.8	1.26	5.8
Valley/Foothill Hardwood	4.6	1.8	0.80	3.7
Wetland	4.6	1.8	1.30	6.0
Delta Vegetation	Long-Term Average ET _o	Precipitation	ET _o F _{max}	Upper Est. ET _c
	ft/yr			ft/yr
Aquatic	4.8	1.2	1.05	5.0
Grassland	4.8	1.2	0.25	1.2
Other Flood Plain Habitat	4.8	1.2	1.27	6.0
Riparian	4.8	1.2	1.35	6.4
Valley/Foothill Hardwood	4.8	1.2	0.80	3.8
Wetland	4.8	1.2	1.36	6.5
San Joaquin Basin Vegetation	Long-Term Average ET _o	Precipitation	ET _o F _{max}	Upper Est. ET _c
	ft/yr			ft/yr
Aquatic	4.7	1.0	1.05	4.9
Grassland	4.7	1.0	0.21	1.0
Other Flood Plain Habitat	4.7	1.0	1.22	5.7
Riparian	4.7	1.0	1.27	5.9
Valley/Foothill Hardwood	4.7	1.0	0.80	3.7
Wetland	4.7	1.0	1.30	6.1

The upper ET_c estimates shown in Table 8 are based on annual computations for average ET_o within each basin. A more detailed evaluation is planned in the near future to examine long-term average weather parameters for multiple weather stations within each basin to refine these estimates. Additional refinements include possibly subdividing each basin by localized weather conditions (precipitation and ET_o) and using remote sensing of actual evapotranspiration to

examine the relative ET_c rates for vegetative habitat that might be similar to what would have been found in pre-development. Through these refinements the Upper and Lower ET_c estimates in the following section could change especially the Lower ET_c estimates which are conservatively low for some vegetation such as grasslands.

3.1.6.4 Calculation of natural outflow

Natural flows are those that would have occurred before the Central Valley was altered by colonial and American development. The primary reason natural flows are lower than unimpaired flows is water use by natural vegetation is not accounted for in the unimpaired flow calculation. To get a truer estimate of natural flows, an estimate may be calculated by subtracting natural vegetation water use from the total supply using a simple water balance around the portion of the Central Valley that drains to the Bay:

$$\text{Delta Outflow} = \text{Water Supply} - \text{Water Use by Native Vegetation}$$

The water balance was calculated for the portion of the Central Valley that drains to the Bay as defined by DWR's unimpaired flow calculations. The results of the natural outflow calculation are summarized in Table 10. This calculation adjusts DWR's estimate of unimpaired Delta outflow to account for consumptive use by native vegetation to provide a more accurate estimate of natural annual Delta outflow assuming average climatic conditions over water years 1922-2010.

Water supply was set equal to the sum of DWR's unimpaired Delta inflow and DWR's estimate of precipitation on the valley floor. Natural inflow to the Delta watersheds is assumed to be equal to DWR's unimpaired rim inflow, reported as "Delta Unimpaired Total Inflow" for the period 1922-2010 from the most recent version of DWR's impaired flow calculations. The annual average is 29.2 MAF/yr. Precipitation on the Valley floor estimated using the most recent long-term, annual average (1922-2008) calculated by DWR for use in their C2VSIM groundwater model based on PRISM data (Kadir, 2012). The results of this analysis are summarized in Table 9.

Vegetation water use was determined by multiplying ET_c for each vegetation type by the number of acres in each region. Because of the uncertainties described previously in determining the actual ET_c values from predevelopment vegetation, an upper and lower estimate of ET_c was used to calculate a range of vegetation water use. The lower end of the ET range for riparian forest, wetland, and grassland is as described in Table 6, and is based on reports from field studies.

Other Floodplain Habitat as described by Chico 2003 is a mix of grassland, wetland and riparian land cover. The lower end of the range was determined using best professional judgment. The lower end ET of grassland is 0.8 ft/yr, wetlands is 5.1 ft/yr, and riparian forest is 4.2 ft/yr and so a ET for Other Floodplain Habitat should fall within the above stated range. Historical references indicate that land cover was predominantly dense riparian forest rather than grassland, and therefore it is appropriate to select an ET similar to Valley/Foothill Hardwood (4.0). Using best professional judgment the lower end ET for Valley/Foothill Hardwood is 3.5 ft/yr.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

The lower end of the range for Valley/Foothill Hardwood was increased from 0.9 to 2 in order to reflect the historical studies indicating dense riparian forest. The 0.9 field study was based on areas with large grasslands and few trees.

The natural flow calculation presented here is not an estimate of a realized annual Delta outflow, i.e., it is not an estimate of actual flow in an individual year such as 1900 or 1850. Rather, the natural flow calculation is a long-term annual average, presented to demonstrate that unimpaired flows are natural flows and are an improper basis from which to establish objectives intended to restore the health of the estuary, which evolved in an entirely different flow environment.

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

Table 9 Valley Floor Precipitation (1922-2008)

Region	ValleyFloor Area (Acres)	Long-Term Average Precipitation (in/yr)	Precipitation (ac-ft/yr)
Sacramento Basin	3,712,090	21.3	6,588,960
Delta	1,399,159	14.5	1,690,650
San Joaquin Basin	3,013,204	11.7	2,937,874
Total			11,217,484

Table 10 Estimated Delta Outflow Under Predevelopment Conditions

				Long-Term Average Annual Water Supply (MAF/Yr)	
Water Supply					
Unimpaired Rim Inflow				29.20	
Precipitation on the Valley Floor				11.22	
Total Water Supply				40.42	
ETc Outflow					
Sacramento Basin	Lower ETc	Upper ETc	Area	Lower ETc	Upper ETc
Vegetation	ft/yr	ft/yr	1,000 Acres	MAF/yr	MAF/yr
Aquatic	4.4	4.8	33	0.14	0.16
Grassland	0.8	1.4	1,591	1.32	2.19
Other Flood Plain Habitat	3.5	5.6	475	1.66	2.66
Riparian	4.2	5.8	444	1.86	2.57
Valley/Foothill Hardwood	2.0	3.7	640	1.28	2.35
Wetland	5.1	6.0	530	2.7	3.17
Delta Basin					
Delta Basin	Lower ETc	Upper ETc	Area	Lower ETc	Upper ETc
Vegetation	ft/yr	ft/yr	1,000 Acres	MAF/yr	MAF/yr
Aquatic	4.5	5.0	18	0.08	0.09
Grassland	0.8	1.2	616	0.50	0.73
Other Flood Plain Habitat	3.5	6.0	117	0.41	0.71
Riparian	4.2	6.4	55	0.23	0.35
Valley/Foothill Hardwood	2.0	3.8	198	0.4	0.75

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

Wetland	5.1	6.5	395	2.02	2.55
San Joaquin Basin	Lower ETC	Upper ETC	Area	Lower ETC	Upper ETC
Vegetation	ft/yr	ft/yr	1,000 Acres	MAF/yr	MAF/yr
Aquatic	4.4	4.9	9	0.04	0.05
Grassland	0.8	1.0	2,264	1.80	2.22
Other Flood Plain Habitat	3.5	5.7	572	2.00	3.26
Riparian	4.2	5.9	72	0.3	0.43
Valley/Foothill Hardwood	2.0	3.7	9	0.02	0.03
Wetland	5.1	6.1	86	0.44	0.53
Total Vegetation Water Use				17.20	24.80
				Upper Bound	Lower Bound
				MAF/yr	MAF/yr
		Natural Flow Condition		23.21	15.61

The current outflow based on 2011 level of development as reported by DWR in its SWP Delivery Reliability Report is 16 MAF/yr. The result of this analysis is that current outflow is within this initial estimate of predevelopment annual average outflow. In addition, unimpaired outflow, based on SOURCE, is 28 MAF. The unimpaired outflow estimate is nearly 80% higher than the low estimate of natural outflow and 17% higher than the high estimate. The most important conclusion to be gleaned from this analysis is that unimpaired outflow is not an accurate or meaningful estimate of natural outflow.

3.1.6.5 Description of analysis to refine predevelopment outflow calculation

The Public Water Agencies are developing a simple spreadsheet model that estimates natural Delta inflows and outflows that would have occurred prior to colonial and American settlement (*i.e.*, pre-development conditions). The purpose of this further analysis is to estimate inter- and intra- annual variability in predevelopment or “natural” outflow that was not included in the initial analysis contained above.

Pre-development Delta inflows and outflows will be developed for an 88-year hydrologic period (1922-2009) assuming a monthly time step. The spreadsheet model will allow the user to easily perform sensitivity analysis by changing key input assumptions.

Calculations of pre-development Delta inflows and outflow will modify unimpaired flow calculations undertaken and published by DWR. Specifically, DWR’s estimates of unimpaired flows will be modified to account for: (1) valley floor depletion of water supplies through evapotranspiration of native vegetation and riparian lands; (2) bank overflow and detention

Analytical Tools: Technical Assessment Methods for Evaluating Changes to The Delta Plan

storage in low-lying areas within the Valley floor; and (3) seasonal variation in groundwater storage. In contrast to DWR's unimpaired flow estimates, pre-development accretions within the valley floor will be calculated using a land use based approach. Valley floor depletions will be calculated using estimates of pre-development land use and a simple one-dimensional root zone soil moisture model. Bank overflows and detention storage will be estimated using a hydraulic model of the Sacramento and San Joaquin river system and hydrologic routing of overflows through detention basins. Seasonal variation in groundwater storage will be estimated based on a review of historical literature and depletion by natural vegetation.

Development of Delta inflows and outflows under natural conditions will be undertaken in a series of steps as follows:

- Obtain unimpaired outflows from the mountain and foothill watersheds from published DWR reports and data
- Determine historical accretions within the valley floor
- Adjust historical accretions to account for land use change within the floor of the Central Valley.
- Route unimpaired flows through the stream system, accounting for bank overflow and detention storage
- Determine Delta outflow from Delta inflows and in-Delta depletions

It is anticipated that this model will be completed in early 2013. The Public Water Agencies anticipate having further discussions with State Water Board as the model is finalized and vetted with the scientific community.

Technical Memorandum Nutrient Science Summary

December 21, 2012

Historically, scientists have described primary productivity in the Bay-Delta as not being limited by nutrients (Cloern 2001; Lopez et al. 2006) and not experiencing signs of classic eutrophication (Cloern 2001). However, changes in nutrient loads are affecting ecosystem dynamics in complex ways that extend beyond our historic understanding of the process of eutrophication. Total nutrient load sets the upper limit on total primary production, and ultimately secondary production, and increases in nutrient loading are commonly associated with eutrophication. The most common effects of eutrophication are increased chl-*a* in the water column, development of hypoxia or anoxia (low or no dissolved oxygen, respectively), loss of native submerged aquatic vegetation, increased harmful algal blooms, and changes in biodiversity, including loss of certain fisheries (e.g., Cloern 2001; Anderson et al. 2002).

Nutrient effects on aquatic systems are far more complex and subtle than those normally associated with eutrophication and can occur across the full spectrum of nutrient limitation to nutrient super-saturation (Glibert et al 2012a). Changes in nutrient form (chemical state, oxidized vs. reduced, organic vs. inorganic, dissolved vs. particulate) and the proportion of different elements (including carbon (C), nitrogen (N), phosphorous (P), and silicon (Si), among others) also have effects on ecosystems at both the scale of the primary producers (the algae) and throughout the ecosystem. In the Bay-Delta, the total loads, the forms, and the relative proportions of nutrients have been changing over time. These changes have had profound effects on ecosystem structure of this system, as documented below. This technical memorandum describes the effects of two such changes: the proportion of ammonium to nitrate (NH₄:NO₃) and the proportion of nitrogen to phosphorus (N:P).

Ammonium:Nitrate

For decades, researchers have explored the relative use – or relative preference for – different forms of nitrogen (N) by phytoplankton. Ammonium (NH₄) is generally considered to be the form of nitrogen preferred by phytoplankton due to the more favorable energetics associated with its assimilation compared to that of nitrate (NO₃). It is also well documented that NH₄ can inhibit the uptake of NO₃, but the relative effect of this inhibition is a function of species composition and other environmental factors (Dortch 1990). When NH₄ inhibits the uptake of NO₃ by phytoplankton, it can also exhibit a strong negative control on total productivity (Yoshiyama and Sharp 2006; Dugdale et al. 2007). NH₄ suppression of NO₃ uptake when both nutrients are in ample supply should not be confused with the preferential use of NH₄ by phytoplankton when N is limiting. Under the latter conditions, phytoplankton will use NH₄ preferentially because it requires less energy than NO₃. Under the former conditions, the cells must cope with an excess; and in doing so, their metabolism is less capable of assimilating NO₃.

Within the Bay-Delta's aquatic ecosystems, Dugdale et al. (2007) show that “bloom levels of chlorophyll-*a* are evident only when NO₃ uptake occurs and that NO₃ uptake only takes place at lower ambient NH₄ concentrations.” They conclude that ammonium concentrations greater than 4 μmol L⁻¹ (0.056 mg L⁻¹) inhibit nitrate uptake by diatoms and thus suppress bloom formation. This level of NH₄ is in line with other inhibitory level estimates in the Bay-Delta (Wilkerson, *et al.* 2006; Parker *et al.* 2012a, 2012b; Dugdale *et al.* 2012), in the Delaware Estuary (Yoshiyama and Sharp 2006) and in laboratory experiments with Chesapeake Bay phytoplankton (Lomas and Glibert 1999a).

This level of ammonium is exceeded a majority of the time in the Sacramento River and Suisun Bay. For example, water quality monitoring data for the Bay-Delta show that the ammonium concentrations in the

lower Sacramento River at Hood consistently exceed the ammonium inhibition threshold of $4 \mu\text{mol L}^{-1}$ (equivalent to 0.056 mg L^{-1}), as established by data from the Interagency Ecological Program's Environmental Monitoring Program (Figure 1).

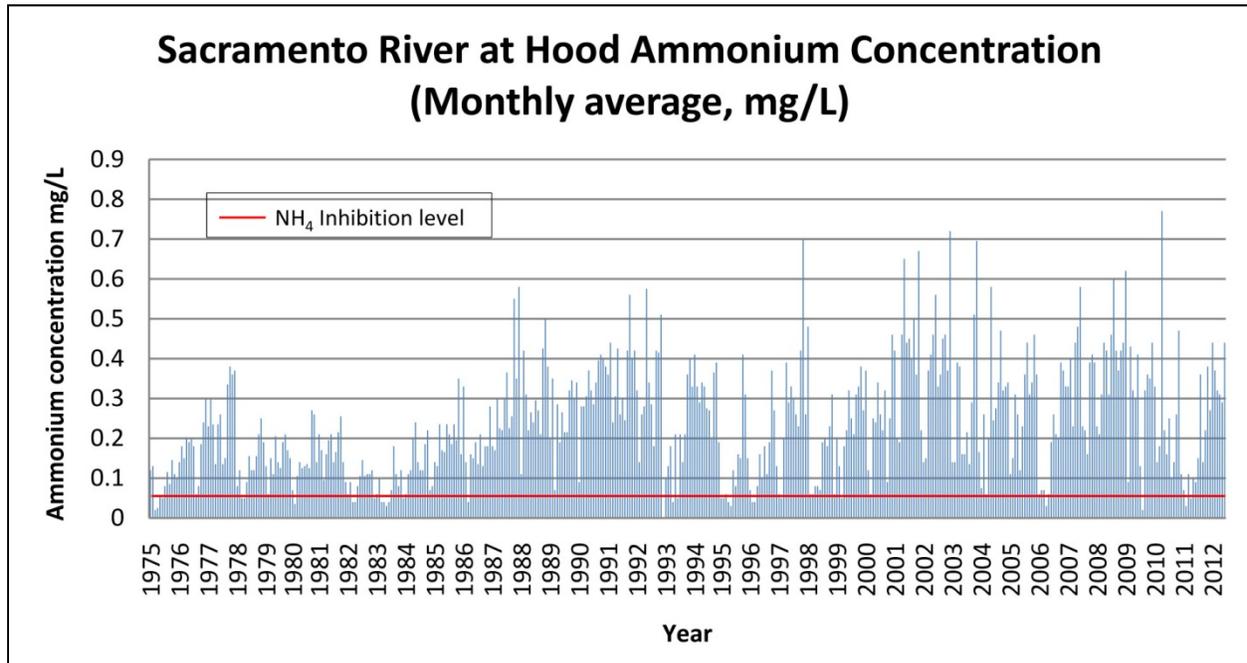


Figure 1. Average monthly ammonium concentration in the lower Sacramento River at Hood. Source: Environmental Monitoring Program data.

The effects of changes in the proportion of $\text{NH}_4:\text{NO}_3$ have been shown for the Bay-Delta in both field observations and laboratory experiments. Parker et al. (2012a) observed a 60% decline in primary production in the Sacramento River below the Sacramento Regional Wastewater Treatment Plant, where NH_4 is discharged, compared to production above the Treatment Plant's outfall. Also supporting this finding, Parker et al. (2012b) found that “[b]y tracing both carbon (C) and N uptake we provide clear evidence that high rates of C uptake are linked to phytoplankton NO_3 , and not NH_4 , use.” They conclude that the increased proportion of NH_4 “may help explain some of the reduced primary production and phytoplankton biomass observed [in the San Francisco Estuary] since the 1970s.”

In enclosure experiments with samples from Central Bay, Suisun Bay, and the Sacramento River at Rio Vista, representing a gradient of both nutrient concentrations and proportions of different forms of N, Wilkerson et al. (in preparation) observed “a gradient of decreasing phytoplankton physiological rates in the upstream direction as far as Rio Vista.” Phytoplankton productivity rates (both carbon and nitrogen uptake) decreased with increasing concentrations of NH_4 .

In a series of recent experiments conducted with natural samples from the Sacramento River, the effects of altered proportions of $\text{NH}_4:\text{NO}_3$ were also apparent (Glibert et al. 2012b). In these experiments, the proportions of these nutrients were manipulated, and both short-term N uptake rates and longer-term N production rates were assessed. Two findings are of note. First, when $20 \mu\text{mol NH}_4$ was added to the sample, a concentration commonly observed in the Sacramento River, and the rate of NO_3 uptake was measured across a concentration gradient, the rate of uptake of NO_3 decreased significantly compared to unamended rates measured over a period of < 1 hour (Figure 2). Second, when samples were enriched with NH_4 , NO_3 , or urea (at the molar equivalent dose) for a period of 24-48 hours, and then rates of

uptake of all N forms measured, the summed rate of N uptake in the NH_4 -added treatment was significantly lower than that in the NO_3 -added or urea-added treatments (Figure 3).

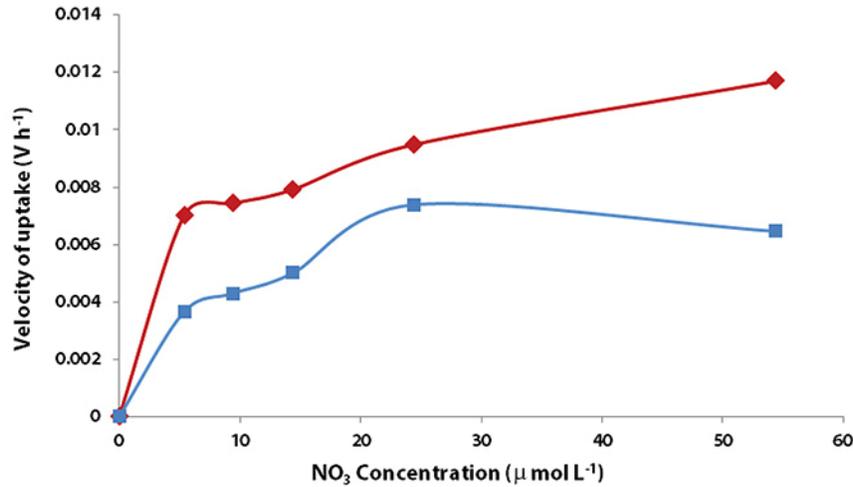


Figure 2. Velocity of uptake of NO_3 as a function of added NO_3 enrichment (red curve), and the same relationship but with a constant addition of $20 \mu\text{mol L}^{-1} \text{NH}_4$ (blue curve). Nitrate uptake is reduced when NH_4 is added. Experiment was conducted with water collected from the Sacramento River. Data from Glibert et al. (2012b).

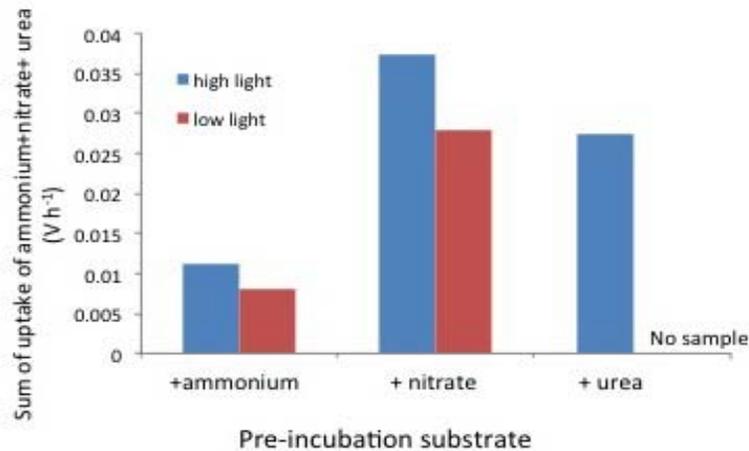


Figure 3. Summed rate of uptake of nitrate+ ammonium+ urea for samples collected from the Sacramento River and pre-incubated with the substrate indicated, after which short-term uptake rates were measured using ^{15}N tracer techniques. The experiment was conducted under both high (blue bars) and low (red bars) irradiance levels. The summed rate of N uptake in the NH_4 -added treatment was significantly lower than that in the NO_3 -added or urea-added treatments. From Glibert et al. (2012b).

This finding is further supported by the 37 years of data collected by the Environmental Monitoring Program in the Bay-Delta. When monthly data of chlorophyll-a and diatom cell count are plotted against ammonium levels for the period 1975 to 2012 there is a marked decreasing trend in both as ammonium

levels rise, with an increasing effect around the 0.056 mg L^{-1} ($4 \mu\text{mol L}^{-1}$) inhibition level (Figures 4 and 5).

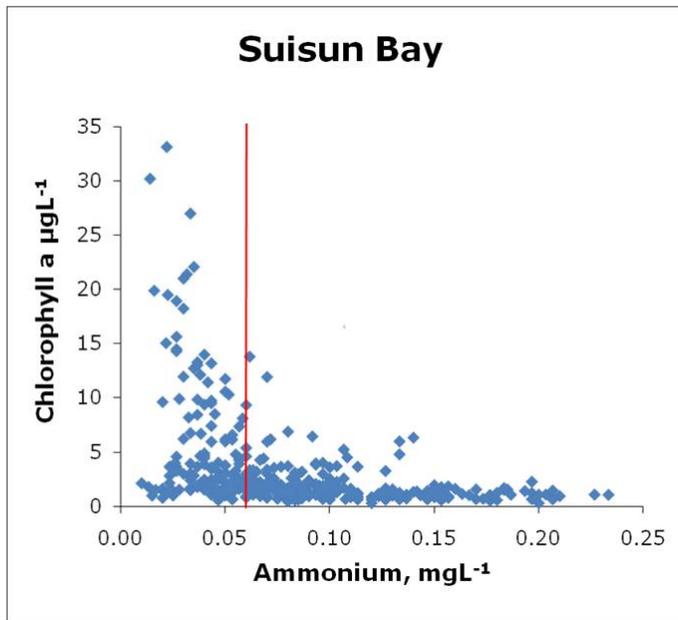


Figure 4. Chlorophyll-*a* concentration plotted with ammonium concentration in Suisun Bay. As NH_4 concentration increases above the level where inhibition is observed (red line at 0.056 mg L^{-1} NH_4), chl-*a* levels decline. (Source: Environmental Monitoring Program data)

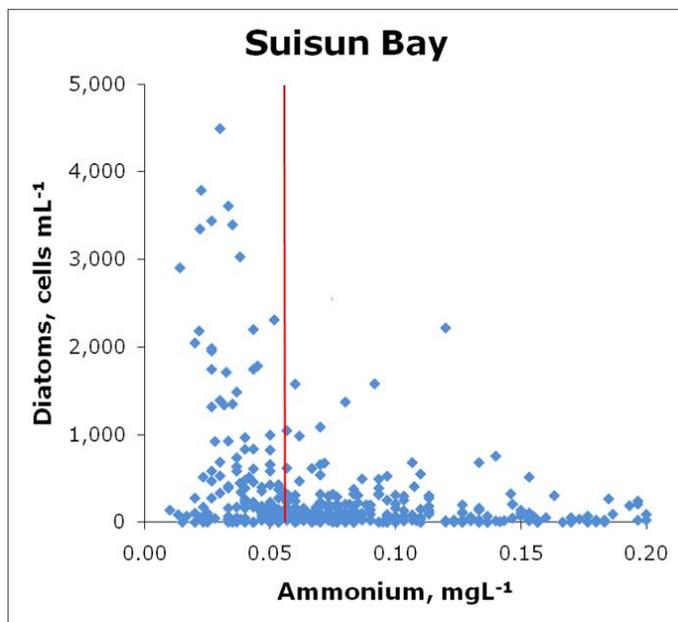


Figure 5. Diatom cell count plotted with ammonium concentration in Suisun Bay. As NH_4 concentration increases above the level where inhibition is observed (red line at 0.056 mg L^{-1} NH_4), diatom abundance declines. (Source: Environmental Monitoring Program data)

These observations of NH_4 suppression are not new in or unique to the Bay-Delta. A large body of scientific research describes NH_4 suppression of algae productivity (*e.g.* Ludwig 1938; Harvey 1953). Some of the early field demonstrations of this phenomenon were carried out by MacIsaac and Dugdale

(1969, 1972), followed by research in the Chesapeake Bay by McCarthy et al. (1975). Maestrini et al. (1982) showed that only after NH_4 concentrations were reduced to $< 7 \mu\text{mol L}^{-1}$ (0.098 mg L^{-1}) was NO_3 uptake sufficient to match that of NH_4 uptake. Price et al. (1985) showed that the rate of NO_3 uptake was reduced ~50% in samples that also received an NH_4 spike compared to those receiving a NO_3 spike. Lomas and Glibert (1999a) described the threshold for inhibition of NO_3 uptake at NH_4 levels of approximately $1 \mu\text{mol L}^{-1}$ (0.014 mg L^{-1}). Yoshiyama and Sharp (2006) saw a “striking decline in production at NH_4 levels above a low threshold (around $10 \mu\text{mol L}^{-1}$)” (0.14 mg L^{-1}). The importance of NH_4 inhibition of NO_3 uptake was considered to be a necessary interaction to include in a recent model of the emergent phytoplankton community in the California Current System (Goebel et al. 2010). In recent experiments conducted in the tidal freshwater estuarine zone of the Guadiana Estuary (Spain and Portugal), it was also found that NO_3 consumption decreased with increasing NH_4 uptake, and these findings were most pronounced during the most productive period. Total primary productivity was suppressed as a result (Domingues et al. 2011). This is particularly problematic for the Bay-Delta as it is already a comparatively low producing estuary (Jassby *et al.*, 2002; Kimmerer *et al.*, 2012). Laboratory experiments suggest that Delta-wide chl-a levels are now low enough to limit zooplankton abundance (Müller-Solger *et al.*, 2002).

The form of N available to a phytoplankton community affects more than just rates of uptake and productivity. Their proportions also affect phytoplankton species composition. The physiological literature strongly supports the concept that different algal communities use different forms of N. Diatoms, once the dominant algal group in the Bay-Delta, generally have a preference for NO_3 ; dinoflagellates and cyanobacteria generally prefer more chemically reduced forms of N (NH_4 , urea, organic nitrogen) (e.g., Berg et al. 2001; Glibert et al. 2004, 2006; Brown 2009). Under some circumstances, diatoms have a physiological requirement for NO_3 (Lomas and Glibert 1999a,b). Moreover, diatoms usually show no evidence of NO_3 uptake saturation under very high NO_3 conditions (Collos et al. 1992, 1997; Lomas and Glibert 1999a), in contrast to the generally accepted saturating uptake kinetic relationships that are used to describe the relationship between nutrients and uptake rate. Cyanobacteria have been shown to preferentially use chemically reduced forms of N, like NH_4 , over NO_3 . Evidence comes from measurements of enzyme activities in the cells (Solomon et al. 2010), directly determined rates of N uptake using isotope tracer techniques (Glibert et al. 2004; Kendall et al. 2011), direct growth studies (Berman and Chava 1999; citations within Meyer et al. 2009), and observations of changes in community composition with enrichment with different forms of N (Domingues et al. 2011).

There is also evidence that the increase in aerial coverage by the invasive aquatic plant *Egeria densa* may be attributed to the ratio of nutrient inputs to the system. Feijoo, et al. (2002) experimentally found that *E. densa* absorbed more nitrogen from water when it was present in the form of NH_4 than when it occurred as NO_3 .

Thus, although there are many factors that regulate the relative contribution of a nutrient source to different phytoplankton groups, and even species-specific differences within groups, it has generally been established that NO_3 disproportionately contributes to diatoms' uptake and production, while reduced forms of N (both NH_4 and urea) disproportionately contribute to the uptake and growth of cyanobacteria. As stated by Domingues et al. (2011), “...increased inputs of N as NH_4 due to urban waste effluents may result in a shift in phytoplankton community composition, towards a dominance of cyanobacteria and green algae.” And, as stated by Lehman et al. (2010), “Recent increases in NH_4 concentration in the western delta may give a competitive advantage to *Microcystis* which rapidly assimilates NH_4 over NO_3 .” The phytoplankton community composition in the Bay-Delta estuary has shifted in just this manner.

The shift in algal community composition in the Bay-Delta has been far more extensive than just the recent increase in annual blooms of *Microcystis*. The Delta's algal species composition has shifted from

diatoms to smaller and lower quality food species such as flagellates, cryptophytes and cyanobacteria (Lehman, 2000; Lehman *et al.*, 2005; Lehman *et al.*, 2010; Jassby *et al.*, 2002; Sommer *et al.*, 2007; Glibert, 2010; Glibert *et al.*, 2011; Winder and Jassby, 2010) and to invasive macrophytes such as *Egeria densa* (Sommer, *et al.*, 2007; Nobriga *et al.*, 2005; Glibert *et al.*, 2011). Jassby (2008) states:

A decrease in percentage of diatom biovolume occurred during 1975–1989, caused by both a decrease in diatoms and an increase in green algae, cyanobacteria, and flagellate species biovolume (Kimmerer 2005; Lehman 1996), i.e., probably in the direction of declining nutritional value per unit biomass. In principle, the total nutritional value of a community could decrease even as its biomass increases. Moreover, changes in size, shape, and motility of species comprising the phytoplankton community could also affect their availability as food particles for crustacean zooplankton and other consumers.

Total Ammonia Toxicity

In addition to altering phytoplankton community structure, growth rates and abundance, total ammonia is also toxic to some higher trophic level organisms. Scientists at UC Davis have investigated the effects of total ammonia to the calanoid copepod *Pseudodiaptomus forbesi* using a full life-cycle bioassay approach (Teh *et al.* 2011). *P. forbesi* is an important prey item for the young of many fish species in the Bay-Delta including delta smelt and longfin smelt (Nobriga 2002; Hobbs *et al.* 2006; Feyrer *et al.* 2003). Teh *et al.* (2011) found that total NH_4 at 0.36 mg L^{-1} ($25.7 \text{ } \mu\text{mol L}^{-1}$) significantly affects the recruitment of new adult copepods and total NH_4 at 0.38 mg L^{-1} ($27.1 \text{ } \mu\text{mol L}^{-1}$) significantly affects the number of newborn nauplii surviving to 3 days (Teh *et al.* 2011). For comparison, monthly water samples collected between 2009-2010 from the Sacramento River between Hood and Isleton, approximately 30 miles downstream from the point of discharge, exceeded this level of NH_4 44% of the time (Figure 6).

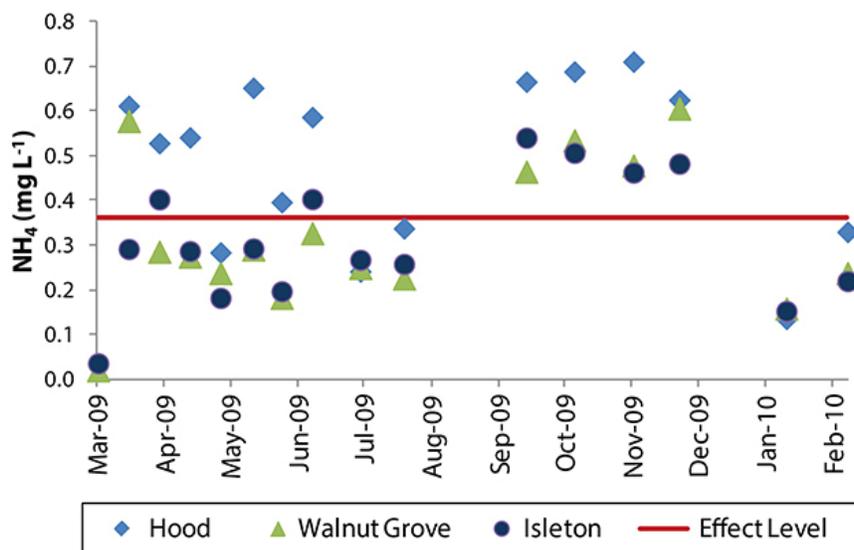


Figure 6. Ammonium concentrations in the Sacramento River measured at Hood, Walnut Grove, and Isleton between 2009 and 2010. Hood and Isleton are approximately 8 and 30 miles downstream of the discharge, respectively. The horizontal line at 0.36 mg L^{-1} is the level at which significant toxicity to copepods is observed. Data from Foe *et al.* (2010).

The Teh et al. (2011) study was recently cited in the U.S. Fish and Wildlife Service 12-month finding on the petition to list the Bay-Delta longfin smelt as threatened or endangered under the ESA. (77 Fed. Reg. 19755, 19776 [April 12, 2012].) The proposed rule states that “[a]quatic insects on which the longfin smelt relies upon for food have been shown to be sensitive to ammonia.” (77 Fed. Reg. 19776.) The proposed rule states that “[a]mmonia also can be toxic to several species of copepods important to larval and juvenile fishes.” (*Id.*) The toxic effect of total ammonia is a major stressor on aquatic life that has a pervasive impact across the Bay-Delta estuary.

Further, the U.S. Environmental Protection Agency’s (USEPA) recently published Bay-Delta Action Plan highlights concerns with aquatic life toxicity caused by total ammonia nitrogen and identifies total ammonia levels as one of the suspected contributors to the pelagic organism decline in the Bay Delta (USEPA 2012). USEPA also proposed updated Ammonia Aquatic Life Criteria in 2009, which are more stringent than existing criteria promulgated in 1999 and consider ammonia toxicity to freshwater mussels (USEPA 2009). In the Bay Delta Action Plan USEPA states that they will finalize the new national ammonia aquatic life criteria and they encourage the Regional Boards to consider adopting the criteria and using the criteria to develop effluent limitations for ammonia.

Nitrogen:Phosphorus

Extensive research has found that the N:P ratio also has profound effects on community structure. The N:P ratio of nutrients has doubled in the Bay-Delta estuary over the last 35 years as is apparent from the data on Figure 7. These increases are a result not only of the increasing total N load (due to increasing effluent as well as other sources), but also as a function of declining P loads (Van Nieuwenhuysse 2007; Glibert 2010, Glibert et al. 2011).

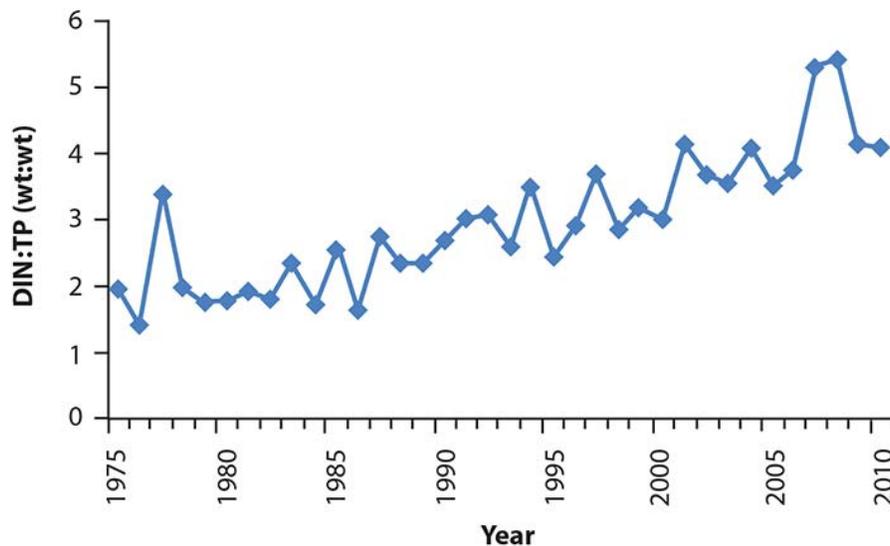


Figure 7. Average annual (March-November) ratio of dissolved inorganic nitrogen to total phosphorus has doubled in the Bay-Delta. (Source: IEP monitoring data from stations in Suisun Bay and the confluence (D4, D6, D7, D8)).

There are a number of strategies available to different types of phytoplankton for coping with an environment where nutrient ratios are not in proportion to their internal requirements (Glibert and Burkholder 2011). For example, cell size is an important determinant of elemental composition (Harris 1986; Finkel et al. 2010). Small cells have a lower requirement for P due to the smaller need for structural

components in the cell (Finkel et al. 2010). In comparison to diatoms, very small cyanobacteria such as *Synechococcus* have a much larger cellular ratio of carbon to phosphorus (C:P), on average (Finkel et al. 2010). This explains why small cells, such as *Synechococcus*, have been found to thrive in waters that are comparatively P poor, as is the case in Florida Bay (Glibert et al. 2004).

There is strong support in the scientific literature for the proposition that the N:P ratio influences phytoplankton community composition. For example, in the Seto Inland Sea of Japan, removal of phosphorus also led to a shift in phytoplankton community structure from “nonharmful diatoms to harmful raphidophytes...and then finally to harmful/toxic dinoflagellates” (Yamamoto 2002). In this case the reduction in phosphorus which increased N:P, led to a change in phytoplankton community composition and was suggested to be “the major cause of the reduction in fishery production” (Yamamoto 2002).

In a retrospective analysis of 30 years of data from the Bay-Delta estuary, Glibert et al. (2011) found that the variation in these nutrient concentrations and ratios is highly correlated to variations in the total amount and composition of phytoplankton. This analysis revealed relationships between biological parameters and nutrients and/or nutrient ratios using both the original data and data that were adjusted for autocorrelation. At the phytoplankton level, as described earlier, there has been a decline in total chl-a and a decline in total diatoms over the past several decades in proportion to the increase in total inorganic N to total P (Figure 8). The change in chl-a with N:P is apparent in different regions of the Bay Delta; as N:P increases, chl-a declines (Figure 9).

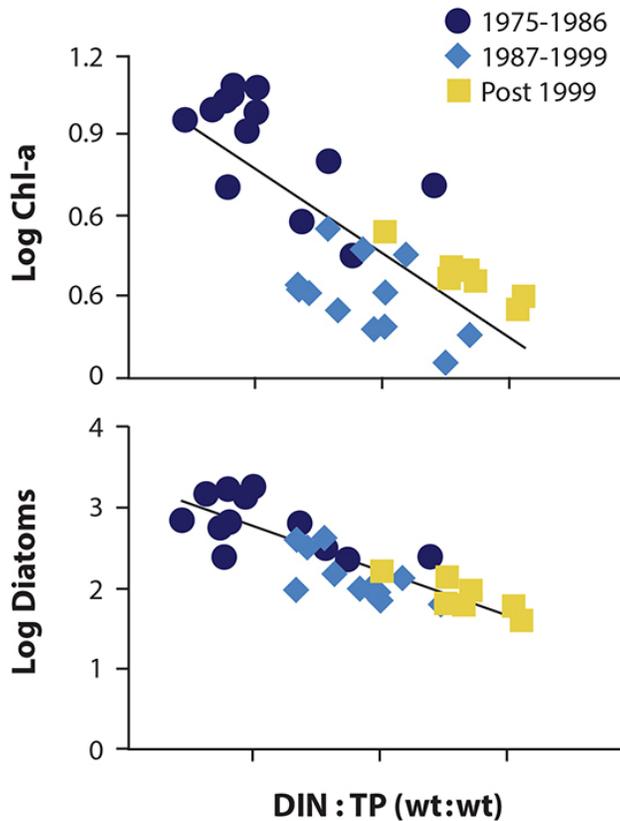


Figure 8. Change in the concentration of chl-*a* ($\mu\text{g L}^{-1}$) and abundance of diatoms (Bacillariophyceae, cells mL^{-1}) as a function of dissolved inorganic N to total phosphorus. A loss of total chl-*a* and a loss of total diatoms in the phytoplankton community have occurred over the past several decades in

proportion to the change in total inorganic N to total P. The relationship is significant at $p < 0.05$. Different periods of time are represented by different symbols: 1975-1986, filled circles; 1987-1999, diamonds; post-1999- filled squares. Data shown are for the years 1975-2005 and cover the region from the confluence to Suisun Bay. All data log-transformed. Data from Glibert et al. (2011).

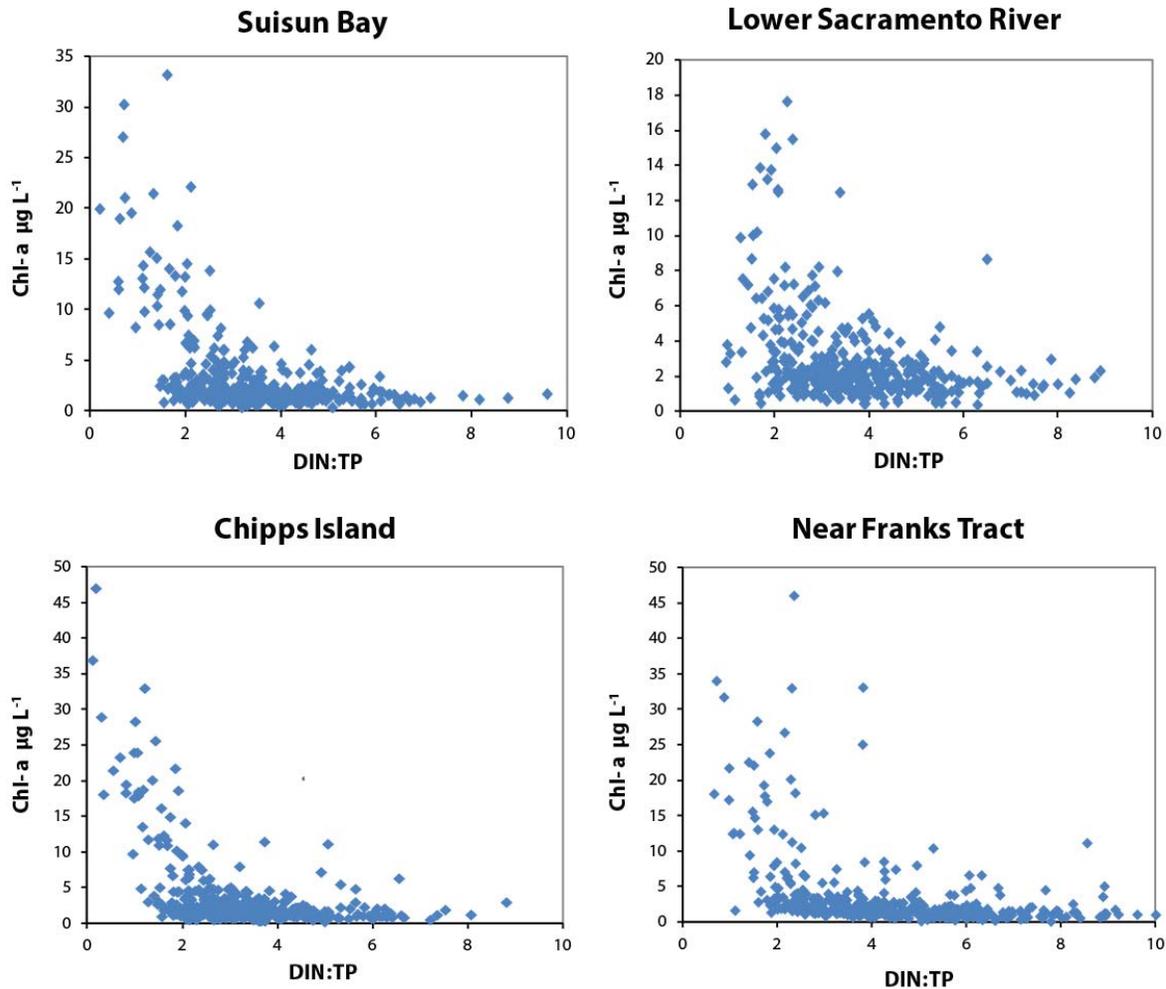


Figure 9. Chl-*a* concentration plotted against DIN:TP for subregions of the Delta, 1975-2011. As DIN:TP increases, there is a loss of chl-*a*. (Source: Environmental Monitoring Program data).

Fast-growing phytoplankton require proportionately more P to satisfy metabolic demands. Diatoms are typically fast-growing, and thus require proportionately more P to meet this metabolic demand. In ecological terms, they are considered a *r*-selected group, would be expected to have a low N:P biomass ratio (due to the high P cellular demand), and thus would be expected to be outcompeted if N:P in the environment increases. So-called *r*-selected species are out-competed when the environment changes (e.g., Heckey and Kilham 1988). In contrast, many cyanobacteria are considered to be *k*-selected, implying a slower growth rate and a higher metabolic N:P. In fact, “Reynolds (1984) singled out *Microcystis* as an example of a *k*-selected phytoplankter because it grows slowly in nature” (Heckey and Kilham 1988).

The balance of N:P can also affect other metabolic aspects of phytoplankton besides growth, including toxin production, cell membrane thickness, and other chemical constituents that have been considered to

turn good food “bad” (Mitra and Flynn 2005). For example, toxin production by numerous harmful algae has been shown to increase when the cells are grown under nutrient-imbalanced conditions and when there is a change in N or P availability (Flynn et al. 1994; Johansson and Granéli 1999; Granéli and Flynn 2006). In Daechung Reservoir, Korea, researchers found that toxicity of cyanobacteria was related not only to an increase in N in the water, but to the cellular N content as well (Oh et al. 2000). A recent report by van de Waal (2009) demonstrated in chemostat experiments that under high carbon dioxide and high N conditions, microcystin (an algal toxin) production was enhanced in *Microcystis*. Similar relationships were reported for a field survey of the Hirosawa-no-ike fish pond in Kyoto, Japan, where the strongest correlations with microcystin were high concentrations of NO_3 and NH_4 and the seasonal peaks in *Microcystis* blooms were associated with extremely high N:P ratios (Ha et al. 2009). Thus, not only is *Microcystis* abundance enhanced under high N:P, but its toxicity appears to be as well (Oh et al. 2000).

It is well accepted that the nutritional value of phytoplankton differs from one species to another. Toxin production can inhibit grazing. Some phytoplankton species are rejected by grazers due to their size. Others vary in their nutritional quality. For example, some diatom species produce certain highly unsaturated fatty acids that are essential for zooplankton reproduction (reviewed by Kilham et al. 1997) while flagellates generally produce different fatty acids than diatoms (Olsen 1999). Many trophic interactions, such as rates of growth or fecundity, are dependent on the acquisition of particular fatty acids, as a measure of the food quality of algae (e.g., Ahlgren et al. 1990; Coutteau and Sorgeloos 1997; Weers and Gulati 1997; Brett and Müller-Navarra 1997). In feeding experiments, Ger et al. (2010) observed reduced survival of the copepods, *Pseudodiaptomus* and *Eurytemora*, even when *Microcystis* was only a small portion of their available diet. Brett and Müller-Navarra (1997) developed a food quality rank for 10 species from 5 major phytoplankton groups based on the average of the observed change in the abundance of individual zooplankters that preyed upon these phytoplankton in growth bioassays. They and others (see Park et al. 2003) have applied a 0-1 scale of phytoplankton food quality in which cyanobacteria ranks at 0.2; green algae, 0.525; diatoms, 0.7; and cryptomonads, 0.95. Thus, a trend of decreasing diatoms and increasing cyanobacteria in the Bay-Delta would suggest, based on these rankings, a decrease in food quality for higher trophic levels.

Cloern and Dufford (2005) state, “[t]he efficiency of energy transfer from phytoplankton to consumers and ultimate production at upper trophic levels vary with algal species composition: diatom-dominated marine upwelling systems sustain 50 times more fish biomass per unit of phytoplankton biomass than cyanobacteria-dominated lakes.”

For species that prey on phytoplankton (e.g., zooplankton), stoichiometry affects all aspects of behavior, such as growth rate, fecundity, and ultimately the success of different populations (Jeyasingh and Weider 2005, 2007), but may affect various life stages differently (Moe et al. 2005, p.31): “[a]n organism’s requirements for different elements may vary throughout its life cycle, and thus certain life stages may be more sensitive than others to variation in the stoichiometry of its resource.” For example, copepod juveniles have a relatively high demand for C, N, and P, but at a later stage, while C is still needed for metabolism, more P must be allocated to eggs. Therefore, P-poor food sources can disproportionately affect egg production while not affecting survival (Faerovig and Hessen 2003; Laspoumaderes et al. 2010). In a laboratory study where *Acartia tonsa* was fed diatoms grown on different N concentrations, Kiørboe (1989), confirmed that this zooplankter changes its feeding rate in response to phytoplankton of different chemical composition – thus, in response to food quality. Moreover, egg production followed the variation in algal N content and increased with increasing algal N. In the Bay-Delta, Slaughter and Kimmerer (2010) observed lower reproductive rates and lower growth rates of the copepod, *Acartia* sp. in the low salinity zone compared to taxa in other areas of the estuary. Their observation may be due to differences in nutrient stoichiometry between these areas.

In a review of field and laboratory-based research on stoichiometry in food webs, Hessen (1997) showed that a shift from copepods to *Daphnia* tracked N:P; copepods retain proportionately more N, while *Daphnia* are proportionately more P rich. Often, those organisms that are most able to retain the nutrient in limited supply, in this case P, have the competitive advantage in an unbalanced system. Glibert et al. (2011) illustrated a finding similar to Hessen's, that the decline in calanoid copepods in the Bay-Delta, and the invasion of cyclopoids tracked N:P over time. Variation in proportional densities of the calanoid copepod *Eurytemora* with the cyclopoid copepod *Limnithona* over time has followed changes in the DIN:TP (dissolved inorganic nitrogen to total phosphorus) ratio (Figure 10), a pattern consistent with these grazers being responsive to changes in elemental stoichiometry and maintenance of altered dynamic equilibria on a long-term scale. In fact, Glibert et al. (2011) found relationships between many zooplankton species and nutrient composition. Results from whole-lake experimentation suggest that the N:P ratio is linked to alterations in zooplankton size, composition, and growth rate, as those animals with increased RNA allocation (more P available for growth) will grow at higher rates due to increased protein synthesis rates (Sterner and Elser 2002, Schindler 1974). Similar findings were reported from annual studies in the Baltic Sea (Walve and Larsson 1999).

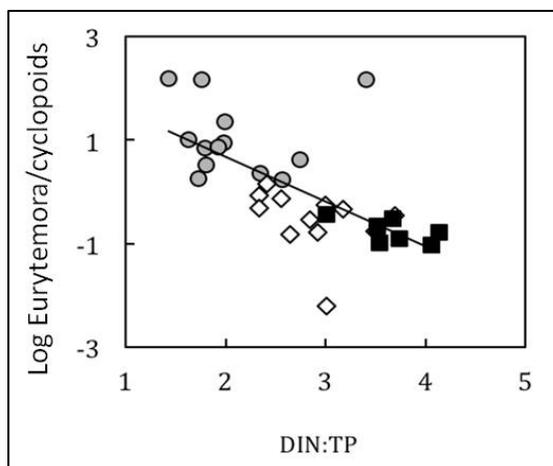


Figure 10. Change in the ratio of *Eurytemora* to cyclopoid copepods (all data log transformed) as a function of DIN:TP for annually averaged data from 1975-2005 for samples collected between the confluence and Suisun Bay. As DIN:TP increases, the proportion of *Eurytemora* to Cyclopoids decreases. Different periods of time are represented by different symbols: 1975-1986, filled circles; 1987-1999, diamonds; post-1999 filled squares. The correlation for these and for data that were detrended (not shown) are significant ($p < 0.05$). From Glibert et al. 2011.

Superimposed on these empirical observations is consideration of whether substrate quality or food quality is altered on an episodic basis, or whether changes are long-term and sustained. As conceptualized by Hood and Sterner (2010), a change in predator growth rate depends on the extent to which a diet is sustained or switches between low-quality food and high-quality food as defined by the relative P content.

Higher Trophic Level Effects

Disproportionate N and P loads are now recognized to have effects at all scales, from genomic to ecosystems that need further empirical resolution (Peñuelas et al. 2012). When N:P availability changes, food webs change, biogeochemical cycling can change, and these changes can be positively reinforcing. Sterner and Elser (2002) state: "[s]toichiometry can either constrain trophic cascades by diminishing the chances of success of key species, or **be a critical aspect of spectacular trophic cascades with large shifts in primary producer species and major shifts in ecosystem nutrient cycling**" [emphasis added]. Just as different elemental ratios may affect the composition of the primary producers, different nutrient

requirements of organisms occupying higher trophic levels will have an impact on their ability to thrive as community composition changes at the base of the food web. At the ecosystem scale, the total load and balance of nutrient elements have effects that propagate through the food web, with the potential of transforming ecosystems to new stable states. Although the shift in algal community composition in terms of diatoms and cyanobacteria has been emphasized above, this shift in the Bay-Delta estuary has been far more complicated. With the decline in water column chl-*a* and an increase in light availability, other primary producers have increased in abundance, including invasive macrophytes such as *Egeria densa* (Sommer et al. 2007; Nobriga et al. 2005; Glibert et al. 2011). *E. densa* may be particularly well suited to the low DIP:DIN environment of the Bay-Delta since it is able to access sediment bound phosphorus through its roots. In fact, similar increases in macrophytes were observed in many other systems in which N:P increased following N enrichment and P reduction, including the Potomac River, Chesapeake Bay, Ebro River in Spain, and the Rhine River in Germany (Glibert et al. 2011; Glibert 2012). Such macrophyte invasions can have profound impacts on ecosystems, not only because they alter the flow of C and the overall productivity of the system, but they also serve as “ecological engineers,” decreasing nutrients through uptake, reducing turbidity by trapping sediments, and providing refuge for zooplankton and habitat for other species, including fish (Yarrow et al. 2009; Glibert 2012).

The interplay between nutrient stoichiometry and biogeochemistry is well illustrated when a system is driven to higher macrophyte productivity. Macrophytes can be highly productive, which can result in elevation of pH due to carbon drawdown in the process of photosynthesis. As noted by Glibert (2012), once pH is elevated, the fundamental physical–chemical relationships related to P adsorption–desorption in sediments change, as does N biogeochemistry (Jordan et al. 2008; Gao et al. 2012). Moreover, under increased pH conditions, the biogeochemistry of calcification is altered, increasing the potential for calcification and the growth of calcifying organisms. Thus, the change in the abundance of the clam *Potamocorbula amurensis* from the time of its introduction in the mid-1980s to 2005 has been shown to be highly and positively correlated to the increase in total N:total P ($r^2 = 0.46$; $n = 20$; $p < 0.01$; all data log transformed), and the average annual abundance of this species has also been found to be highly and positively correlated with mean annual average pH in the estuary ($r^2 = 0.64$; $n = 19$; $p < 0.01$; species abundance data log transformed) (Glibert et al. 2011). Interestingly, the Potomac River, Rhine River and the Ebro River have had similar invasions of macrophytes and *Corbicula* clams that relate to increases in N:P loading (Ibanez et al. 2008; Glibert et al. 2011; Glibert 2012).

In the Bay-Delta estuary, data show top-down grazing of phytoplankton by the clam *P. amurensis* exerts a strong control on phytoplankton biomass, as is also the case for other systems when invaded by bivalve mollusks. Prior interpretations, emphasizing stochastic invasions largely via ballast water exchange imply that the invasive event was the ultimate cause of the change in top-down control of phytoplankton. The ecological stoichiometric interpretation does not preclude strong top-down control of selected component organisms, nor ballast water exchange as the mechanism of introduction. The distinction is that, at the overall ecosystem level, the structuring of species is affected by alterations in nutrients and ecosystem biogeochemistry.

The arguments presented here make the case that bottom-up control contributed to the conditions that allowed *P. amurensis* to become a dominant regulator of phytoplankton production. In other words, invasive species effects and nutrient effects are interrelated. This interpretation is consistent with Ware and Thompson’s (2005) insights from a broad survey of the relative contributions of “bottom-up” vs. “top-down” factors that potentially control fish catch in the coastal waters of the western U.S.; they, too, reported that bottom-up factors were more important.

Several recent reviews have investigated the stoichiometry of fish (Sterner and George 2000; Hendrixson et al. 2007; McIntyre and Flecker 2010). Not only does a strong shift in body N:P occur with growth stage (Pilati and Vanni 2007), but strong differences between taxonomic families also occur. In fact,

Hendrixson et al. (2007) demonstrated, for 20 families of fish, that a phylogenetic tree could be developed based on the body nutrient composition.

In the Bay-Delta estuary, numerous changes in fish community composition occurred in relation to phytoplankton and zooplankton changes, and to N:P (Glibert 2010; Glibert et al. 2011) (Figure 11). Glibert et al. (2011) also found that total P “explained at least as much of the variability in delta smelt as did the [Feyrer et al. 2011] habitat index, and dinoflagellate abundance explained even more.” Unlike correlations with Bay-Delta outflow or with the location of the 2 practical salinity unit isohaline, where the underlying mechanisms driving the correlations are largely unknown, the nutrient relationships have a strong mechanistic explanation in ecological stoichiometry and stable state principles. For this reason, there is relatively low uncertainty that changes in nutrient stoichiometry in the Bay-Delta estuary, achieved through both external forces (altered land-based nutrient loads) and internal, organism-driven, assimilative and dissimilative processes, are related to community compositional changes (Glibert et al. 2011; Glibert 2012).

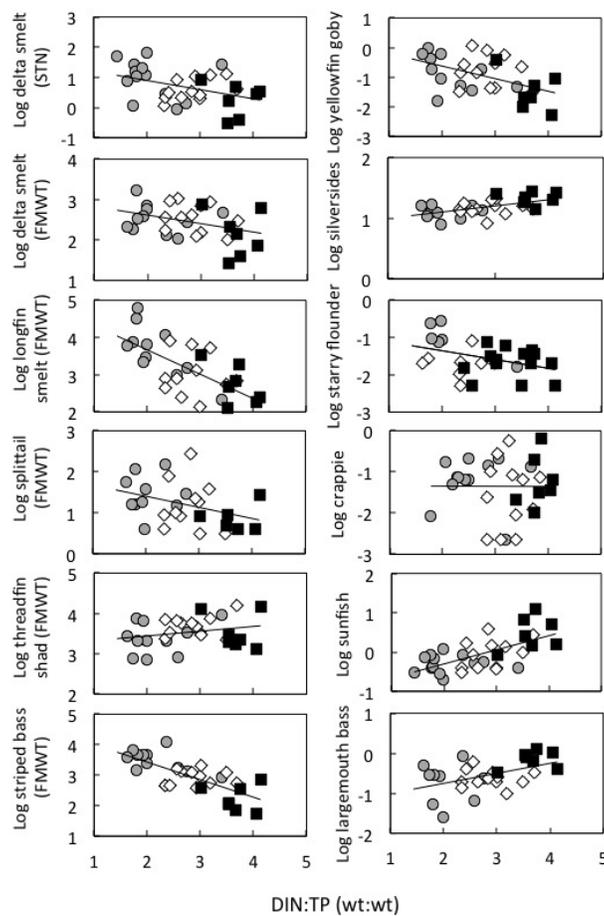


Figure 11. Changes in the abundance of major fishes in relation to ratio of dissolved inorganic nitrogen to total phosphorus from 1975-2005. Different periods of time are represented by different symbols: 1975-1986, filled circles; 1987-1999, diamonds; post-1999 filled squares. All data were log-transformed. The correlations for all fish except crappie were significant ($p < 0.05$) in these data as well as in data that were detrended. Source: Glibert et al. (2011).

Total Nutrient Loads

Total nutrient load sets the upper limit on total primary production, and increases in nutrient loading are commonly associated with eutrophication. Nutrient levels in water diverted from the Delta are at concentrations that can produce nuisance algal and aquatic weed growth and adversely affect drinking water beneficial uses in downstream conveyance facilities and reservoirs. Algal and aquatic plant growth in the SWP conveyance facilities and downstream reservoirs is neither light limited nor inhibited by high ammonium concentrations since most of the ammonium from the Delta has been nitrified to nitrate. Elevated levels of nutrients (phosphorus and nitrogen compounds) stimulate nuisance algal and aquatic weed growth that includes production, by specific cyanobacteria, of noxious taste and odor compounds and algal toxins. In addition to algal produced taste and odor and algal toxin concerns, increases in algal and aquatic weed biomass can impede flow in conveyances, shorten filter run times and increase solids production at drinking water treatment plants, and add to organic carbon loading.

Frequently annual phosphorus concentrations at Clifton Court Forebay have averaged 0.11 mg/L and total nitrogen has averaged 0.87 mg L⁻¹. Phosphorus is significantly higher than the 0.020 to 0.042 mg L⁻¹ that has been associated with a high risk of nuisance growth and eutrophication (USEPA 1980, 2001a). Levels of both nutrients exceed USEPA Ecoregion I phosphorus and total nitrogen reference conditions of 0.047 mg L⁻¹ and 0.31 mg L⁻¹, respectively (USEPA 2001b)¹. Ecoregion I includes the Central Valley.

Literature values and USEPA's ecoregion reference conditions² provide a starting point for determining whether nutrient concentrations in Delta waters are at levels that could cause water quality impairments, such as algal production of compounds that produce noxious tastes and odors. More importantly, there is already significant evidence of nutrient-related adverse impacts from Delta water. Through 2006, the Department of Water Resources (DWR) has applied algicide treatments to Clifton Court Forebay for aquatic weeds and algae multiple times each summer. This practice was halted in 2007, however, over concerns of potential impacts to listed fish species. DWR has also treated the South Bay Aqueduct (SBA) to control algae that are stimulated by nutrient-rich Delta water. Including preventative treatments, DWR has treated the SBA for algal control between 10 and 16 times per year in recent years. Periodic treatment of the California Aqueduct and State Water Project (SWP) terminal reservoirs is also necessary for the same reason. Given the increasing environmental concerns about the use of copper-based algaecides, it is likely that effective control will become increasingly more difficult and reduce the ability of downstream users to manage algae-related problems in the future.

Eutrophication, ecological stoichiometry and alternate stable state theories combine to serve as a unifying framework for understanding the complexity of responses not only in the Bay-Delta estuary but also, more generally, in many comparative systems. This interpretation does not negate the importance of ecological invasions, habitat changes, multiple stressors and food-web complexities, but adds an explanatory mechanism to those interpretations through biogeochemistry and organismal stoichiometry. Ecological stoichiometry affects systems by setting elemental constraints on the growth of organisms. This, in turn, affects food quality and the relationships between predators and prey.

Examples of Responses to Nutrient Load Reductions

A growing body of literature documents improvements in ecosystem functions where nutrient loading is reduced and stoichiometric balance is restored. Reducing nutrient loading in the Chesapeake Bay, Tampa Bay, and coastal areas of Denmark has proven to be effective at reversing the harmful effects of previously undertreated discharges and restoring the native food webs. For example, within several years of increasing nutrient removal at the Blue Plains treatment plant in Washington D.C., N:P ratios in the

¹ The reference condition is the 25th percentile of the nutrient data for sites within the ecoregion and is meant to represent the nutrient concentrations in minimally impacted water bodies.

² Significant questions have been raised about the use of reference conditions to establish regulatory criteria for nutrients. Nevertheless, they provide a starting point for evaluating water quality.

Potomac River declined, the abundance of the invasive *Hydrilla verticillata* and *Corbicula fluminea* began to decline (Figure 12 showing *Corbicula Fluminea* and other relationships with N:P), and the abundance of native grasses increased (Ruhl and Rybicki 2010).

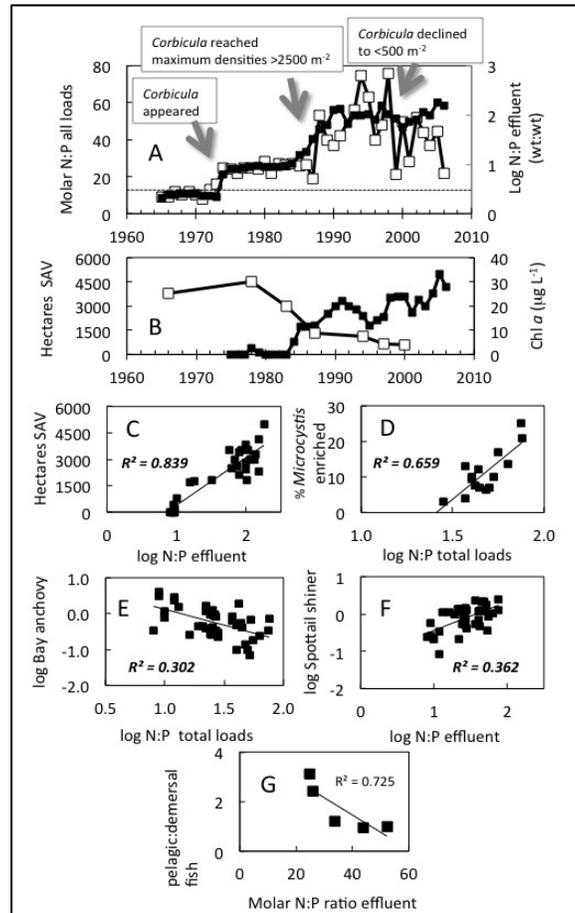


Figure 12. Comparative relationships for the Potomac River. Panel A shows the change in effluent N loading and the relative abundance of the invasive clam, *Corbicula fluminea*. *C. fluminea* appeared coincident with a sharp increase in N:P and increased in abundance as N:P increased. When N:P decreased sharply around 1999, *C. fluminea* abundance also declined sharply from >2500 m⁻² to <500 m⁻². Data derived from Dresler and Cory (1980), Jaworski et al. (2007), and Cummins et al. (2010). Figure reproduced from Glibert et al. (2011).

Tampa Bay provides another important example. Eutrophication problems in Tampa Bay were severe in the 1970s, with N loads approximating 24 tons per day, about half of which was due to point source effluent (Greening and Janicki 2006). Several years after nitrogen and phosphorus reductions were achieved, native seagrass began to increase. Lower nutrient discharges also had positive effects on the coastal waters around the island of Funen, Denmark (Rask et al. 1999). Since the mid 1980s, there has been a roughly 50% reduction in the loading of N and P in the region due to point source reductions. Again, native grasses returned and low oxygen problems were reversed.

Cloern (2001) provides additional examples of recovery following reductions in nutrient and waste inputs. Citing other researchers, Cloern (2001) shows improvements in dissolved oxygen levels in the Forth Estuary in Scotland following improvements in wastewater treatment. Citing a second study, Cloern

(2001) shows increases in fish diversity in the Thames Estuary following improvements in wastewater treatment there (Figure 13).

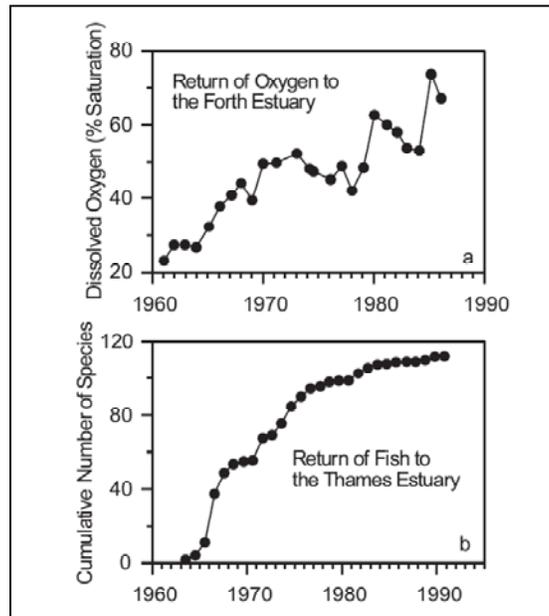


Figure 13. Two examples of recovery following actions to restore water quality in estuaries impacted by nutrient and waste inputs: (a) trend of increasing dissolved oxygen concentration (summer months) in the Forth Estuary, Scotland, following Improvements in wastewater treatment; (b) trend of increasing diversity of fishes in the Thames Estuary following implementation of advanced wastewater treatment and increases in oxygen concentrations (Source: Figure 20 from Cloern 2001).

Moreover, there is recent evidence that diatom blooms may be restored in the Bay-Delta estuary if NH_4 loading is reduced. In Suisun Bay, an unusual diatom bloom in Spring 2000 reached chl-*a* concentrations of $30 \mu\text{g L}^{-1}$ when NH_4 concentrations declined to $1.9 \mu\text{mol L}^{-1}$ (0.027 mg L^{-1}) (Wilkerson et al. 2006). Similarly, chl-*a* concentrations in Suisun Bay reached $35 \mu\text{g L}^{-1}$ during spring 2010 when NH_4 concentrations declined to $0.5 \mu\text{mol L}^{-1}$ (0.007 mg L^{-1}) (Dugdale et al. 2011, 2012). These blooms are comparable to spring chl-*a* levels from 1969 to 1977 (Ball and Arthur 1979) when NH_4 concentrations were $1.8 \mu\text{mol L}^{-1}$ (0.025 mg L^{-1}) during summer and $4.0 \mu\text{mol L}^{-1}$ (0.056 mg L^{-1}) during winter (Cloern and Cheng 1981).

Additionally, as Glibert (2010) reported, “[s]upporting the idea that correct balance of nutrients is important for restoration of delta smelt and other pelagic fish, there is a small but apparently successful subpopulation of delta smelt in a restored habitat, Liberty Island. Liberty Island is outside the immediate influence of Sacramento River nutrients. It has abundant diatoms among a mixed phytoplankton assemblage, as well as lower NH_4 levels and higher ratios of $\text{NO}_3:\text{NH}_4$ than the main Sacramento River [citations removed].”

REFERENCES

- Ahlgren, G., L. Lundstedt, M. Brett, and C. Forsberg. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *Journal of Plankton Research* 12: 809-818.
- Anderson, D. M., P. M. Glibert, and J. M. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25: 704-726.
- Ball, M.D. and J. F. Arthur. 1979. Planktonic chlorophyll dynamics in the Northern San Francisco Bay and Delta. Pacific Division of the American Association for the Advancement of Science c/o California Academy of Sciences Golden Gate Park San Francisco, California 94118.
- Berg, G.M., P.M. Glibert, N.O.G. Jorgensen, M. Balode and I. Purina. 2001. Variability in inorganic and organic nitrogen uptake associated with riverine nutrient input in the Gulf of Riga, Baltic Sea. *Estuaries*, 24: 176-186
- Berman, T and S. Chava, 1999. "Algal growth on organic compounds as nitrogen sources." *Journal of Plankton Research*, 21:1423-1437.
- Brett M.T. and D.C. Müller-Navarra. 1997. The role of highly un-saturated fatty acids in aquatic food-web processes. *Freshwater Biology* 38: 483-499.
- Brown, T. 2009. Phytoplankton community composition: The rise of the flagellates. *IEP Newsletter*. 22(3):20-28.
- Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecological Progress Series* 210: 223-253.
- Cloern, J.E and R.T. Cheng. 1981. Simulation model of *Skeletonema costatum* population dynamics in Northern San Francisco Bay, California. *Estuarine, Coastal and Shelf Science*. 12:83-100
- Cloern, J.E. and R. Dufford. 2005. Phytoplankton community ecology: principles applied in San Francisco Bay. *Marine Ecology Progress Series*, 285:11-28.
- Collos, Y., M.Y. Siddiqi, M.Y. Wang, A.D.M. Glass, and P.J.Harrison. 1992. Nitrate uptake kinetics by two marine diatoms using the radioactive tracer ^{13}N . *Journal of Experimental Marine Biology and Ecology* 163: 251-260.
- Collos, Y., A. Vaquer, B. Bibent, G. Slawyk, N. Garcia, and P. Souchu. 1997. Variability in nitrate uptake kinetics of phytoplankton communities in a Mediterranean coastal lagoon. *Estuarine, Coastal and Shelf Science* 44: 369-375.
- Coutteau P. and P. Sorgeloos. 1997. Manipulation of dietary lipids, fatty acids and vitamins in zooplankton cultures. *Freshwater Biology* 38: 501-512.
- Cummins, J., C. Buchanan, C. Haywood, H. Moltz, A. Griggs, R. C. Jones, R. Kraus, N. Hitt, and R. V. Bumgardner. 2010. Potomac Basin Large River Environmental Flow Needs. ICPRB Report 10- 3. Interstate Commission on the Potomac River Basin.
- Domingues, R.B., A.B. Barbosa, U. Sommer, and H.M. Galvao. 2011. Ammonium, nitrate and phytoplankton interactions in a freshwater tidal estuarine zone: potential effects of cultural eutrophication. *Aquatic Science* 73: 3331-343.
- Dortch, Q. 1990. The interaction between ammonium and nitrate uptake in phytoplankton. *Marine Ecological Progress Series* 61:183-201.
- Dresler, P. V. and R. L. Cory. 1980. The Asiatic clam, *Corbicula fluminea* (Müller), in the tidal Potomac River, Maryland. *Estuaries*, 3: 150-152).

- Dugdale, R.C., F. P. Wilkerson, V. E. Hogue and A. Marchi. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. *Estuarine, Coastal and Shelf Science*, 73: 17-29.
- Dugdale, R., F. Wilkerson, A. Parker. 2011. Brief report in response to selected issues raised by Sacramento Regional County Sanitation District in petition for review of discharge permit issued by the Central Valley Regional Water Quality Control Board. May 4, 2011.
- Dugdale, R.C., Wilkerson, F.P., Parker, A.E., Marchi, A., Taberski, K. 2012. River flow and ammonium discharge determine spring phytoplankton blooms in an urbanized estuary. *Estuarine and Coastal Shelf Science*.
- Færøvig, P.J. and D.O. Hessen. 2003. Allocation strategies in crustacean stoichiometry: the potential role of phosphorus in the limitation of reproduction. *Freshwater Biology* 48: 1782-1792.
- Feijoó, C., M.E. García, F. Momo and J.Toja. 2002. Nutrient absorption by the submerged macrophyte *Egeria densa* planch.: effect of ammonium and phosphorus availability in the water column on growth and nutrient uptake. *Limnetica* 21(1-2): 03-104.
- Feyrer F., B. Herbold, S.A. Matern, and P.B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277-288.
- Finkel Z.V., J. Beardall, K.J. Flynn, A. Quiqq, T.A. Rees, J.A. Raven. 2010. Phytoplankton in a changing world: Cells size and elemental stoichiometry. *J. Plankt. Res.*2010, 32: 119-137.
- Flynn, K., J.M. Franco, P. Fernández, B. Reguera, M. Zepata, G. Wood, and K.J. Flynn, 1994. Changes in toxin content, biomass and pigments of the dinoflagellate *Alexandrium minutum* during nitrogen refeeding and growth into nitrogen and phosphorus stress. *Marine Ecological Progress Series* 111: 99-109.
- Foe, C., A. Ballard, and S. Fong. 2010. Nutrient Concentrations and Biological Effects in the Sacramento-San Joaquin Delta. Report prepared for the Central Valley Regional Water Quality Control Board.
- Gao, Y., J. Cornwell, D. Stoecker, and M. Owens. 2012. Effects of cyanobacterial-driven pH increases on sediment nutrient fluxes and coupled nitrification-denitrification in a shallow fresh water estuary. *Biogeosciences*, 9:2697-2710.
- Ger, K.A., S.J. Teh, D.V. Baxa, S. Lesmeister, and C.R. Goldman. 2010. The effects of dietary *Microcystis aeruginosa* and microcystin on the copepods of the upper San Francisco Estuary. *Freshwater Biology*, 55:1548-1559.
- Glibert, P., 2010. Long-term changes in nutrient loading and stoichiometry and their relationships with changes in the food web and dominant pelagic fish species in the San Francisco Estuary, California. *Reviews in Fisheries Science*. 18(2):211-232.
- Glibert, P.M. 2012. Ecological stoichiometry and its implications for aquatic ecosystem sustainability. *Current Opinion Envir. Sustainability* 4:272-2.
- Glibert and Burkholder. 2011. Harmful algal blooms and eutrophication: Strategies for nutrient uptake and growth outside the Redfield comfort zone. *Chinese J. Limnol. Oceanogr.* 29: 724-738.
- Glibert, P., C.A. Heil, D. Hollander, M. Revilla, A. Hoare, J. Alexander, S. Murasko. 2004. "Evidence for dissolved organic nitrogen and phosphorous uptake during a cyanobacterial bloom in Florida bay." *Mar Ecol Prog Ser*, 280:73-83.
- Glibert, P.M., J. Harrison, C.A. Heil, and S. Seitzinger. 2006. Escalating worldwide use of urea – a global change contributing to coastal eutrophication. *Biogeochem.*, 77: 441-463.

- Glibert, P.M., D. Fullerton, J.M. Burkholder, J.C. Cornwell, and T.M. Kana. 2011. Ecological stoichiometry, biogeochemical cycling, invasive species, and aquatic food webs: San Francisco Estuary and comparative systems. *Reviews in Fisheries Science*, 19(4): 358-417.
- Glibert, P.M., T.M. Kana, K. Brown. 2012a. From limitation to excess: the consequences of substrate excess and stoichiometry for phytoplankton physiology, trophodynamics and biogeochemistry, and the implications for modeling. *Journal of Marine Systems*, <http://dx.doi.org/10.1016/j.jmarsys.2012.10.004>.
- Glibert, P.M., R.C. Dugdale, A.E. Parker, F. Wilkerson, J. Alexander, S. Blaser, E. Kress, and S. Murasko. 2012b. Elevated ammonium concentrations inhibit total nitrogen uptake and growth, not just nitrate uptake. Poster presentation at Interagency Ecological Program Annual Workshop, April 2012, Folsom, CA.
- Goebel, N.L., C.A. Edwards, J.E. Zehr, and M.J. Follows. 2010. An emergent community ecosystem model applied to the California Current System. *Journal of Marine Systems* 83: 211-242.
- Granéli E., and K. Flynn. 2006. Chemical and physical factors influencing toxin content. In: Granéli E, Turner, J.T. (Eds.), *Ecology of Harmful Algae*. Springer, Heidelberg, pp. 229-241.
- Greening, H. and A. Janicki. 2006. Toward reversal of eutrophic conditions in a subtropical estuary: Water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. *Environ. Mgt.* 38(2):163-178.
- Ha, J.H., T. Hidaka, and H. Tsuno. 2009. Quantification of toxic *Microcystis* and evaluation of its dominance ratio in blooms using real-time PCR. *Envir. Sci. Technol.* 43: 812-818.
- Harris, G.P. 1986. *Phytoplankton Ecology: Structure, Function and Fluctuation*. Cambridge University Press, Cambridge.
- Harvey, H.W. 1953. Synthesis of Organic Nitrogen and Chlorophyll by *Nitzschia Closterium*. *J. Mar. Biol. Res. Assoc. U.K.* 31:477-487.
- Hecky, R.E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* 33:796-822.
- Hendrixson, H. A., R. W. Sterner, and A. D. Kay. 2007. Elemental stoichiometry of freshwater fishes in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* 70: 121-140.
- Hessen, D.O.. 1997. Stoichiometry in food webs – Lotka revisited. *Oikos* 79: 195-200.
- Hobbs, J.A., W.A. Bennett, and J.E. Burton. 2006. Assessing nursery habitat quality for native smelts (*Osmeridae*) in the low-salinity zone of the San Francisco estuary. *Journal of Fish Biology*, 69: 907–922
- Hood, J.M., and R.W. Sterner. 2010. Diet mixing: Do animals integrate growth or resources across temporal heterogeneity? *The American Naturalist* 176: 651-663.
- Ibanez, C., N. Prat, C. Duran, M. Pardos, A. Munne, R. Andreu, N. Caiola, N. Cid, H. Hampel, R. Sanchez, and R. Trobajo. 2008. Changes in dissolved nutrients in the lower Ebro river: Causes and consequences. *Limnetica.* 27(1):131-142.
- Jassby, A. 2008. Phytoplankton in the Upper San Francisco Estuary: recent biomass trends, their causes, and their trophic significance. *San Francisco Estuary and Watershed Science.* 6(1): Article 2, February 2008.
- Jassby, A.D., J.E. Cloern and B.E. Cole. 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnol. Oceanogr.*, 47(3): 698–712.

- Jaworski, N., W. Romano, and C. Buchanan. 2007. The Potomac River Basin and its estuary: Landscape loadings and water quality trends 1895-2005.
- Jeyasingh, P. D., and L.J. Weider. 2005. Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*. *Ecology Letters* 8: 1021-1028.
- Jeyasingh, P. D. and L.J. Weider. 2007. Fundamental links between genes and elements: evolutionary implications of ecological stoichiometry. *Molecular Ecology* 16: 4649-4661.
- Johansson, N. and E. Granéli. 1999. Cell density, chemical composition and toxicity of *Chrysochromulina polylepsis* (Haptophyta) in relation to different N:P supply ratios. *Marine Biology* 135: 209 - 217.
- Jordan, T. E., J. C. Cornwell, W. R. Boynton, and J. T. Anderson. 2008. Changes in phosphorus biogeochemistry along an estuarine salinity gradient: the iron conveyor belt. *Limnology and Oceanography* 53: 172-184.
- Kendall, C., P. Lehman, S.R. Silva, M.B. Young, and M. Guerin. 2011. Tracing sources of nutrients fueling *Microcystis* blooms in the Sacramento-San Joaquin Delta using a multi-fingerprinting approach. Draft report to California Department of Water Resources (unpublished)..
- Kilham, S. S., D.A. Kreeger, C.E. Goulden, and S.G. Lynn. 1997. Effects of nutrient limitation on biochemical constituents of *Ankistrodesmus falcatus*. *Freshwater Biology* 38: 591-596.
- Kimmerer W.J., A.E. Parker, U.E. Lidström, and E.J. Carpenter. 2012. Short-Term and Interannual Variability in Primary Production in the Low-Salinity Zone of the San Francisco Estuary. *Estuaries and Coasts* ,35:913–929.
- Kjørboe, T. 1989. Phytoplankton growth rate and nitrogen content: Implications for feeding and fecundity in a herbivorous copepod. *Marine Ecological Progress Series* 55: 229-234.
- Laspoumaderes, C., B. Modenutti and E. Balseiro. 2010. Herbivory versus omnivory: linking homeostasis and elemental imbalance in copepod development. *Journal of Plankton Research* 32: 1573-1582.
- Lehman, P. W. 2000. The influence of climate on phytoplankton community biomass in San Francisco Bay Estuary. *Limnol. Oceanogr.* 45: 580–590
- Lehman, P. W., G. Boyer, C. Hall, S. Waller and K. Gehrts. 2005. Distribution and toxicity of a new colonial *Microcystis aeruginosa* bloom in the San Francisco Bay Estuary, California. *Hydrobiologia*, 541:87-99
- Lehman, P.W., S.J. Teh, G.L. Boyer, M.L. Nobriga, E. Bass, and C. Hogle. 2010. Initial impacts of *Microcystis aeruginosa* blooms on the aquatic food web in the San Francisco Estuary. *Hydrobiologia*, 637:229-248
- Lomas, M.W. and P.M. Glibert. 1999a. Interactions between NH₄⁺ and NO₃⁻ uptake and assimilation: comparison of diatoms and dinoflagellates at several growth temperatures. *Marine Biology*, 133:541-551.
- Lomas, M.W. and P.M. Glibert. 1999b. Temperature regulation of nitrate uptake: A novel hypothesis about nitrate uptake and reduction in cool-water diatoms. *Limnol Oceanogr*, 44:556-572.
- Lopez, C.B., J.E. Cloern, T.S. Schraga, A.J. Little, L.V. Lucas, J.K. Thompson, and J.R. Burau. 2006. Ecological values of shallow-water habitats: implications for the restoration of disturbed ecosystems. *Ecosystems* 9: 422–440.
- Ludwig, C.A. 1938. The availability of different forms of nitrogen to a green alga (*Chlorella*) *Am.J.Bot.* 25:448-458.
- MacIsaac, J.J. and R.C. Dugdale. 1969. The kinetics of nitrate and ammonium uptake by natural populations of marine phytoplankton. *Deep-Sea Res.* 16:45-67.

- MacIsaac, J.J. and R.C. Dugdale, 1972. Interactions of light and inorganic nitrogen controlling nitrogen uptake in the sea. *Deep-Sea Res.* 19:209-232.
- Maestrini, S. Y., J.M. Robert, I. Truquet. 1982. Simultaneous uptake of ammonium and nitrate by oyster-pond algae. *Mar Biol. Lett.* 3: 143-153.
- McCarthy, J.J., W.R. Taylor and J.L. Taft, 1975. The dynamics of nitrogen and phosphorous cycling in the open water of the Chesapeake Bay. In: T.M. Church (ed.) *Marine Chemistry in the Coastal Environment*. American Chemical Society Symposium Series 18. Washington D.C., pp. 664-681.
- McIntyre, P. B., and A. Flecker. 2010. Ecological stoichiometry as an integrative framework in stream fish ecology. *American Fisheries Society Symposium* 73: 539-558.
- Meyer, J.S., P.J. Mulholland, H.W. Paerl, and A.K. Ward. 2009. "A framework for research addressing the role of ammonia/ammonium in the Sacramento-San Joaquin Delta and the San Francisco Bay Estuary ecosystem." Report to CalFed Science Program.
- Mitra, A. and K.J. Flynn. 2005. Predator-prey interactions: is "ecological stoichiometry" sufficient when good food goes bad? *Journal of Plankton Research* 27: 393-399.
- Moe, S. J., R.S. Stelzer, M.R. Forman, W.S. Harpole, T. Daufresne and T. Yoshida. 2005. Recent advances in ecological stoichiometry: insights for population and community ecology. *Oikos* 109: 29-39.
- Müller-Solger, A., A.D. Jassby and D.C. Müller-Navarra. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). *Limnol Oceanogr.* 47(5):1468-1476.
- Nobriga, M.L. 2002. Larval delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. *California Fish and Game* 88:149-164.
- Nobriga, M.L., F. Feyrer, R.D. Baxter, and M. Chotkowski. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. *Estuaries*, 28(5):776-785.
- Oh, H-M., S.J. Lee, M-H. Jang and B-D. Yoon. 2000. Microcystin production by *Microcystis aeruginosa* in a phosphorus-limited chemostat. *Appl. Environ. Microbiol.* 66: 176-179.
- Olsen, Y., 1999. Lipids and essential fatty acids in aquatic food webs: what can freshwater ecologists learn from mariculture? In: Arts, M.T., Wainman, B.C. (Eds.) *Lipids in Freshwater Ecosystems*. Springer-Verlag, New York, pp. 161-202.
- Park, S., M.T. Brett, E.T. Oshel and C.R. Goldman. 2003. Seston food quality and *Daphnia* production efficiencies in an oligo-mesotrophic subalpine lake. *Aquatic Ecology* 37: 123-136.
- Parker, A.E., R.C. Dugdale, and F.P. Wilkerson. 2012a. Elevated ammonium concentrations from wastewater discharge depress primary productivity in the Sacramento River and the Northern San Francisco Estuary. *Marine Pollution Bulletin*. doi:10.1016/j.marpolbul.2011.12.016.
- Parker, A.E., V. E. Hogue, F.P. Wilkerson, and R.C. Dugdale. 2012b. The effect of inorganic nitrogen speciation on primary production in the San Francisco Estuary. *Estuarine, Coastal and Shelf Science*.
- Peñuelas, J., J. Sardans, A. Rivas-Ubach and I.A. Janssens. 2012. The human-induced imbalance between C, N and P in Earth's life system. *Global Change Biology* 18: 3-6.
- Pilati, A. and M.J. Vanni. 2007. Ontogeny, diet shifts, and nutrient stoichiometry in fish. *Oikos* 116: 1663-167.

- Price, N.M., W.P. Cochlan and P.J. Harrison. 1985. Time course of uptake of inorganic and organic nitrogen by phytoplankton in the Strait of Georgia: comparison of frontal and stratified communities. *Mar. Ecol. Prog. Ser.* 27: 39-53.
- Rask, N., S. E. Pedersen, and M. H. Jensen. 1999. Response to lowered nutrient discharges in the coastal waters around the island of Funen, Denmark. *Hydrobiologia* 393: 69–81.
- Reynolds, C. S. 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. *Freshwater Biol.*, 14, 111–142.
- Ruhl, H.A. and N.B. Rybicki. 2010. Long-term reductions in anthropogenic nutrients link to improvements in Chesapeake Bay habitat. www.pnas.org/cgi/doi/10.1073/pnas.1003590107.
- Schindler, D. W. 1974. Eutrophication and Recovery in Experimental Lakes: Implications for Lake Management. *Science*. 184(4139):897-899.
- Slaughter, A. and W. Kimmerer. 2010. Abundance, composition, feeding, and reproductive rates of key copepod species in the food-limited Low Salinity Zone of the San Francisco Estuary. Poster Presentation at the 6th Biennial Bay-Delta Science Conference, Sacramento, CA, September 27-29, 2010.
- Solomon, C.M., J.L. Collier, G.M. Berg and P.M. Glibert. 2010. Role of urea in microbial metabolism in aquatic systems: a biochemical and molecular review. *Aquatic Microbial Ecology*, 59: 67-88.
- Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries*, 32(6):270-277.
- Sterner, R.W. and J.J. Elser. 2002. *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, N.J.
- Sterner, R. W. and N.B. George. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. *Ecology*, 81, 127-140.
- Teh, S., I. Flores, M. Kawaguchi, S. Lesmeister and C. Teh. 2011. Full Life-Cycle Bioassay Approach to Assess Chronic Exposure of *Pseudodiaptomus forbesi* to Ammonia/Ammonium. Report Submitted to Chris Foe and Mark Gowdy at the State Water Resources Control Board, August 31, 2011.
- U.S. Environmental Protection Agency. 1980. Trophic State of Lakes and Reservoirs, Technical Report E-80-3.
- U.S. Environmental Protection Agency. 2001a. Ambient Water Quality Criteria Recommendations: Information Supporting the Development of State and Tribal Nutrient Criteria; Rivers and Streams in Ecoregion I. U.S. Environmental Protection Agency, Office of Water, EPA 822-B-01-012 (December 2001).
http://www.epa.gov/waterscience/criteria/nutrient/ecoregions/rivers/rivers_1.pdf
- U.S. Environmental Protection Agency. 2001b. Ambient Water Quality Criteria Recommendations: Rivers and Streams in Ecoregion I. U.S. Environmental Protection Agency, Office of Water (December 2001).
- U.S. Environmental Protection Agency. 2009. Draft 2009 Update aquatic life ambient water quality criteria for ammonia- freshwater. EPA-822-D-09-001. [Available at <http://www.epa.gov/waterscience/criteria/ammonia/2009update.pdf>]
- U.S. Environmental Protection Agency. 2012. Water Quality Challenges in the San Francisco Bay/Sacramento-San Joaquin Delta Estuary: EPA's Action Plan. [Available at <http://www.epa.gov/sfbay-delta/pdfs/EPA-bayareaactionplan.pdf>]

- U.S. Fish and Wildlife Service. 2012. Endangered and Threatened Wildlife and Plants; 12-month Finding on a Petition to List the San Francisco Bay-Delta Population of the Longfin Smelt as Endangered or Threatened. 50 CFR Part 17, Docket No. FWS-R8-ES-2008-0045, 4500030113. 77 Fed. Reg. 19755, 19776.
- Van de Waal, D. B., J. M. Verspagen, M. Lurling, E. Van Donk, P. M. Visser and J. Huisman. 2009. The ecological stoichiometry of toxins produced by harmful cyanobacteria: An experimental test of the carbon-nutrient balance hypothesis. *Ecology Letters* 12: 1326-1335.
- Van Nieuwenhuysse, E. 2007. Response of summer chlorophyll concentration to reduced total phosphorus concentration in the Rhine River (Netherlands) and the Sacramento-San Joaquin Delta (California, USA). *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1529-1542.
- Walve, J. and U. Larsson. 1999. Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. *Journal of Plankton Research* 21: 2309-2321.
- Ware, D. M., and R. E. Thompson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science*: 308: 1280-1284.
- Weers, P.M.M. and R.M. Gulati. 1997. Effects of the addition of polyunsaturated fatty acids to the diet on the growth and fecundity of *Daphnia galeata*. *Freshwater Biology*: 38, 721-729.
- Wilkerson, F.P, R.C. Dugdale, V.E. Hogue and A. Marchi. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. *Estuaries and Coasts*, 29(3): 401–416.
- Wilkerson, F.P., A.E. Parker, and R.C. Dugdale. (in preparation). Application of enclosure experiments to characterize potential phytoplankton productivity in rivers and estuaries.
- Winder, M. and A.D. Jassby. 2010. Shifts in zooplankton community structure: Implications for food web processes in the Upper San Francisco Estuary. *Estuaries and Coasts*. DOI 10.1007/s12237-010-9342-x.
- Yamamoto, T. 2002. The Seto Inland Sea—eutrophic or oligotrophic? *Marine Pollution Bulletin* 47(1): 37 – 42.
- Yarrow, M., V. H. Marin, M. Finlayson, A. Tironi, L. E. Delgado, and F. Fischer. 2009. The ecology of *Egeria densa* Planchón (Liliopsida: Alismatales): A wetland ecosystem engineer? *Revista Chilena de Historia Natural* 82: 299-313.
- Yoshiyama, K. and J.H. Sharp. 2006. Phytoplankton response to nutrient enrichment in an urbanized estuary: apparent inhibition of primary production by overeutrophication. *Limnology and Oceanography* 51: 424-434.