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FELLOWSHIP APPLICATION COVER PAGE

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APPROVAL SIGNATURES

FELLOW: [signature]

Name: Monika Winder
Position/Titl PostDoc/PhD
Departmen John Muir Institute of the Environment
Institution: University of California, Davis
Address: One Shields Ave
City, State : Davis, CA, 95616
Telephone: 530 754 9354
Fax: 530 754 6354
E-mail: mwinder@ucavis.edu

MENTOR/PRINCIPAL INVESTIGATOR: [signature]

Name: Geoffrey Schladow
Position/Title: Director, Professor
Department: Civil & Environmental Engineering
Institution: University of California, Davis
Address: One Shields Ave
City, State & : Davis, CA, 95616
Telephone: (530) 752-6932
Fax: 530 754 6354
E-mail: gschladow@ucdavis.edu

AUTHORIZED INSTITUTIONAL REPRESENTATIVE: [signature]

Name: DANIELLE NEFF
Position/Title: Contracts and Grant Analyst
Department: Office of Research, Sponsored Programs
Institution: UC DAVIS
Address: 1850 Research Park Drive, Suite 300
City, State & Zip: Davis, CA 95616
Telephone: 530 - 747 - 3920
Fax: 530 - 747 - 3957
E-mail: dvneff@ucdavis.edu

Will animal subjects be used? ☐ Yes ☒ No

APPROVAL DATE: ______ PROTOCOL #: ______ PENDING: ______

Does this application involve any recombinant DNA technology or rese ☐ Yes ☒ No

Plankton dynamics in the Sacramento−San Joaquin Delta: Long-term trends and trophic interactions

2a. Introduction, Questions and Objectives of the Proposed Research

INTRODUCTION

Estuarine ecosystems play an essential role for human life, provide habitat for numerous organisms, and goods and services with high economic values (Lotze *et al.* 2006). The upper San Francisco Estuary, including the Sacramento−San Joaquin Delta and Suisun Bay and Marsh (hereafter collectively referred to as the 'Delta') has become a focal point for understanding complex ecological interactions associated with human activities and climate change. For the last five decades, a near-continuous ecological data set has been amassed and population declines of many pelagic organisms, including primary producers, zooplankton, and fish have been documented, suggesting that the carrying capacity of the Delta's ecosystem to sustain pelagic biota may have been significantly degraded (summarized in Baxter *et al.* 2007). Pelagic organisms decline has motivated research to identify processes underlying the trends and knowledge garnered from these studies has formed the foundation upon which the *CALFED* and other management and restoration efforts for the Delta are being based. The decadal-scale coherence of pelagic organisms declines across different trophic levels (Kimmerer 2004, Cloern 2007) suggests that any change at the base of the food web propagate up to higher trophic levels (Bouley & Kimmerer 2006, Gaines *et al.* 2006). Primary consumers (zooplankton) are a critical trophic link for energy transfer to upper trophic levels and a key food source for threatened and endangered fish species in the Delta. *Yet long-term trends and patterns for primary producers and mechanisms that regulate their abundances remain largely unstudied in this ecosystem despite the fact that the importance of zooplankton forage for fish has been recognized as one potential major component for the observed fish declines (Baxter et al. 2007).*

Historical data analysis of phytoplankton showed high spatial and temporal variability (Jassby *et al.* 2002, Jassby 2008), however the plankton data set has not been fully utilized to understand detailed responses of zooplankton and their interactions with primary producers and environmental variables in the historical context, although a well-documented records of species counts exists. Because the zooplankton community is vital for ecosystem productivity at higher trophic levels, it is timely to take advantage of this historical data resource to understand long-term variability and processes underlying changes in zooplankton to prevent or ameliorate further fish decline and restore ecosystem productivity. *The proposed research aims to understand trends and processes at the base of the Delta's food web by capitalizing on the comprehensive long-term plankton data set. Retrospective food-web analysis will provide important information to better understand the mechanisms by which changes in the primary prey of pelagic fishes contribute to the long-term and more recent drastic decline of fish species of concern.*

The major goal of this proposed study is to identify spatial and temporal plankton variability and biotic interactions by quantitatively analyzing the taxonomically, 33-year plankton data set. The objectives outlined below will help to improve our knowledge about ecological processes underlying the decline of pelagic organisms; in particular it will *(1)* describe spatial and temporal trends in zooplankton, the major food source for native fish species, *(2)* provide a better understanding of the linkages between phytoplankton biomass and zooplankton production, and *(3)* determine how changes in phytoplankton and zooplankton functional groups relate to biotic interactions and environmental changes. We propose that through integrating plankton variability into the management and restoration plan for the Delta, the dynamics of the ecosystem can be viewed from a new perspective that has key implications for understanding the decline in pelagic organisms. As such, this analysis will produce important input to accomplish the *CALFED* mission (CALFED 2000) and for various Delta planning activities to increase pelagic productivity, including the Action Plan for Pelagic Organisms Decline, Delta Vision, or the Delta Regional Ecosystem Restoration Implementation Plan (Baxter *et al.* 2007).

STUDY SITE AND CORE MONITORING DATA SET

Study site: The San Francisco Estuary, including the San Francisco Bay and the Delta is the largest estuary on the US Pacific coast and provides important ecosystem services to the state of California, including supply of drinking water to over 22 million people, irrigation water for one of the world's most productive agricultural centers, and 26,000 ha of open-water habitat for waterfowl and 130 species of fish (Lucas & Cloern 2002, Sobczak *et al.* 2002). The structure and function of the Delta ecosystem changed statically over the last 150 years and all of the Delta's original 1,400 km^2 of tidal marsh have been drained or diked (Nichols *et al.* 1986), and the tributary rivers have been dammed, channelized, and disconnected from their floodplains. River flow is partially controlled by an extensive system of dams, water diversions, and flood channels. The Estuary receives runoff from a 163,000 km^2 watershed. External river inputs are dominated by the Sacramento and San Joaquin Rivers, which provide on average 84 % and 12 % of the Delta's freshwater, respectively (Gaines *et al.* 2006). Flow rates exhibit considerable seasonal and annual variation and reflect wet winters and dry summers linked to large-scale climate oscillations (Kimmerer 2004). As a result water residence time varies greatly across years and stations. Much of the variability of pelagic organisms in the Delta is associated with hydrology, for example high hydrological variability strongly affects phytoplankton biomass through fluctuations in flushing and growth rates through fluctuations in transparency (Jassby 2008), and it can be expected that flow rates will also affect zooplankton community dynamics.

External river inputs account for 60 % of annual organic matter supply to the Delta; in contrast primary producers within the system account for 15 %. Autochtonous primary production is dominated by phytoplankton, while production by macrophytes and benthic algae is relatively small (Cloern 2001). The habitat types in the Delta are open systems where pelagic food-supply is provided both by import from connecting habitats as well as from internal production (Lucas & Cloern 2002, Cloern 2007).

This study will focus on the Delta, a heterogeneous environment of tidal freshwater habitats, including channels, sloughs, shallow lakes, and estuarine embayments, connecting a 1.6 x 10^7 ha watershed to the San Francisco Bay (Jassby & Cloern 2000). Water salinity varies widely within the system, ranging from fresh in the Delta to coastal salinities near the mouth of the Bay to sometimes hypersaline conditions during droughts in southern parts of the Bay. The boundary between the limnetic (salinity of 0-0.5) and oligohaline (salinity of 0.5-5) zones during median flow conditions is at Chipps Island, near the confluence of the Sacramento and San Joaquin Rivers (for map see Kimmerer 2004).

In addition to human-induced disturbances the ecosystem has been changed due to accelerating invasion of non-native species (Cohen & Carlton 1998). As of 2002, a total of 234 exotic species established in the ecosystem, including plants, protists, invertebrates, and vertebrates. Some of the most widespread invaders that vastly changed ecosystem processes include the suspension-feeding clam *Corbula amurensis* (Alpine & Cloern 1992, Jassby *et al.* 2002), which suppressed phytoplankton production. The zooplankton community also changed significantly due to the introduction of various copepod species including *Pseudodiaptomus forbesi, Eurytemora affinis,* and *Limnoithona tetraspine*, which all have established large populations (Orsi & Ohtsuka 1999, Bouley & Kimmerer 2006). These invaders feed at various trophic levels and largely increase the competition for food resources with native species. For instance the non-native clams compete with zooplankton for algae (Bennett *et al.* 2002) and exotic fishes compete with native fishes for invertebrate prey (Bennett *et al.* 2002).

The long-term declining trend of the pelagic fish species in the estuary (Bennett *et al.* 2002, Baxter *et al.* 2007), including Delta smelt (*Hypomesus transpacificus*), longfin smelt (*Spirinchus thaleichthys*), striped bass (*Morone saxatlis*), and Chinook salmon (*Oncorhynchus tshawytscha*) is to a large part associated with variation of outflow in the estuary. However, abundances of these species declined sharply around 2000 despite relatively moderate hydrology (Baxter *et al.* 2007). Because these fish species show vast differences in their individual life histories (Moyle 2002), it is expected that a combination of factors contribute to the recent collapse and that the environmental conditions such as habitat quality and/or zooplankton forage have fundamentally changed in the Delta.

The water quality data show that in addition to reduced pelagic productivity, the Delta as a whole is becoming saltier, warmer, and more transparent (Kimmerer 2004, Dettinger 2005). These changes are associated with a shift in the seasonal pattern of freshwater inflow to the Delta, and an increase in freshwater export over the last decades (Cayan *et al.* 2001, Dettinger *et al.* 2004). Due to warming trends of the regional climate, the timing of runoff peaks shift towards earlier in the season. The long-term trend of increasing water clarity is largely attributed to reduced sediment input presumably due to dam construction (Kimmerer 2004, Jassby 2008).

<u>Core data for the proposed research:</u> Among the most detailed of the long-term data sets available in ecology is that collected in the Bay-Delta from before 1975 through the present. The comprehensive monitoring activities are managed by the Interagency Ecological Program (IEP; www.iep.water.ca.gov), a consortium of state and federal agencies. Major physical, chemical, and biological parameters have been monitored regularly at approximately monthly intervals since 1975 (Kimmerer 2004, Hennessy & Hieb 2007). This discrete sampling program has used consistent methods since their inception, although the number and distributions of stations have hanged in some cases. In addition abiotic variables (e.g., temperature, salinity, turbidity, flow rates) are measured at high frequency (around every hour) at few stations. The California Department of Fish and Game (DFG) are responsible for collecting zooplankton and the water quality data, while the California Department of Water Resources (DWR) is responsible for phytoplankton and additional water quality data collections. The USGS program for the San Francisco Bay also extends into the Delta at Rio Vista. This historical data set is exceptional in its temporal and spatial coverage, consistency over time and multiplicity of measured variables.

PROPOSED RESEARCH

High temporal variability in estuarine ecosystems poses a challenge for observing and understanding causes and consequences for ecosystem dynamics. Long-term ecological research is of importance to extract seasonal, interannual and inter-decadal variability from random noise and to emphasize underlying processes. Analysis of the Delta's historical data set were especially instructive demonstration of the utility of this type of research (e.g., Jassby & Cloern 2000, Bennett *et al.* 2002, Jassby *et al.* 2002, Kimmerer *et al.* 2005, Cloern *et al.* 2007) and results from those done clearly indicate their value. Outstanding examples of the value of such studies include the decadal-scale investigation of primary producers in the Delta and San Francisco Bay (Jassby *et al.* 2002, Cloern *et al.* 2007, Jassby 2008). These studies demonstrate that impacts operating at different time scale affect ecosystem dynamics, indicating the importance of long-term data analysis. The focus on decadal-scale analysis in the Delta research has mainly concentrated on identifying patterns in abiotic factors, including change in salinity, nutrient concentration, suspended material as well as on primary producers and pelagic fish organisms (see overview in Baxter *et al.* 2007). Except for a few studies on the identification of major zooplankton trends and change in community composition (Kimmerer *et al.* 1994, Orsi & Ohtsuka 1999, Bouley & Kimmerer 2006, Cloern 2007), detailed zooplankton patterns and quantitative food-web linkages remain largely unstudied. With the availability of detailed long-term data sets of major components of the pelagic food web, environmental variables, and sophisticated time series analysis we have a set of established tools to evaluate trophic linkages in the Delta's pelagic food web in a comprehensive fashion. The dynamics of pelagic estuarine communities and biotic interactions will be better understood by applying such a food-web modeling approach and will equip us better with management tools to restore ecosystem function and structure.

The proposed study will fill the gap of knowledge of spatial and temporal patterns in zooplankton variability and interactions within the planktonic community and the environment. In year 1 spatiotemporal variation and trends of zooplankton will be identified and year 2 will concentrate on interactions between phytoplankton, primary consumers and environmental variables.

***Objective 1*: Identification of long-term spatial and temporal patters in zooplankton**

Background – Zooplankton transfer energy from primary (phytoplankton) and bacterial production to higher trophic levels such as fish and are thus an important link in the aquatic food web. All Delta fish species that have declined in abundance have pelagic-feeding larval stages (e.g., Chinook salmon) and some species feed on zooplankton through their entire life history; for example copepods are the primary dietary components for delta smelt (Nobriga 1998). This indicates that zooplankton production will be important for fisheries restoration.

The zooplankton community in the Delta is dominated by rotifers, cladocerans, copepods, and mysids (Table 1). Previous analysis indicated that cladocerans are abundant in spring, whereas copepods do not exhibit clear seasonal patterns (Obrebski *et al.* 1992). There is however high spatial and seasonal variability in the abundance of copepod species among the estuary habitats. Substantial changes in abundance and species composition due to species invasion from East Asia have occurred over the last three decades (Orsi & Ohtsuka 1999), resulting in apparent changes in trophic structure. The sampling period before 1987 was characterized by declines in many species in the Delta (Obrebski *et al.* 1992, Kimmerer *et al.* 1994) including rotifers, cladocerans, and copepod species (Kimmerer 2004, Cloern 2007). Potential reasons for the decline are attributed to reduced phytoplankton biomass, increased export pumping, reduced organic input, or effects of toxic compounds. Over the same time period introduced cyclopoid copepod species, including *Oithona davisae* and *Limnoithona sinensis* increased significantly.

Since the late 1980s the zooplankton fauna underwent substantial changes mainly associated with species introductions. Abundances of *Eurytemora affinis* and *Acartia* spp. declined sharply due to the effects of clam introduction (Bennett *et al.* 2002) and subsequent decline in phytoplankton availability (Jassby *et al.* 2002). The copepod *Pseudodiaptomus forbesi* was first recorded in this estuary in 1988 and is now the dominant calanoid copepod of the low-salinity zone in terms of biomass. The calanoid copepods *P. forbesi* and *E. affinis* are an important food source for key fish species and previous analysis showed that both species have significantly declined at almost all long-term monitoring stations over the last decades (Fig. 1). The small cyclopoid copepod *Limnoithona tetraspina* (length 0.5 mm) has become the numerically dominant copepod since its introduction in 1993 in the low-salinity regions (Bouley & Kimmerer 2006). It feeds primarily upon ciliates and microflagellates, but unlike *P. forbesi*, it is relatively impervious to predation by clams or fish. Low selectivity of fish for this cyclopoid copepod species suggests that it may not be an important food resource for visually-selective fish (Bouley & Kimmerer 2006) and energetically a dead end for the food web. This suggests that zooplankton species composition is a useful indicator of the food quality for fish. Thus, in addition to zooplankton declines, displacement of nutritious by low-nutritious zooplankton forage is likely another underlying factor for the observed fish declines (Baxter *et al.* 2007).

These general trends and patterns of the zooplankton community illustrate that the zooplankton community changed substantially over the last decades. In addition to long-term interannual fluctuations, estuarine environments exhibit strong seasonal variability (Winkler *et al.* 2003, Islam *et al.* 2006), which likely affect seasonal zooplankton abundances. As a result, food availability for native fish species may vary greatly on a seasonal basis resulting in potential mismatch between fish larvae development and zooplankton forage. Life histories of fish species of concern have been described in the Delta (Moyle 2002, Baxter *et al.* 2007) and understanding long-term seasonal zooplankton variability will be crucial to identify potential disruption between the zooplankton-fish trophic link.

To understand spatial and temporal long-term trajectories of zooplankton species and functional groups the following questions will be addressed:

(1a) **What are the long-term trends of Delta's zooplankton community and can distinct sub-regions be identified that show similar patterns?**

Rationale. The Delta is a heterogeneous environment that experiences various degrees of environmental change at different time scales (Kimmerer 2004) and thus high temporal and spatial variability in zooplankton dynamics can be expected. Preliminary trend analysis of zooplankton species showed that the majority of zooplankton species declined significantly at all sampling stations; some species maintained their abundances in specific regions over the record period, while few species showed an increasing trend (see preliminary analysis in Fig. 2). This part of the project will identify long-term zooplankton temporal patterns at Delta-wide scale. Due to large environmental heterogeneity large differences can be expected within stations, thus sub-regions that have experienced similar zooplankton trajectories will be identified, which is expected to result in a clearer picture.

Focal zooplankton response variables will be of two general types: single taxon abundance, and aggregate community properties, including total zooplankton biomass and functional groups. Functional groups will be categorized according to (*a*) feeding ecology (i.e., herbivores, omnivores, predators) and (*b*) nutritional value as forage for fish (i.e., low nutritious vs. high nutritious). The latter category will be a useful indicator on how food quality for fish species changed, which largely depends on zooplankton species composition (Bouley & Kimmerer 2006). Zooplankton nutritious value for fish will be based on fish preference outcome from experiments and energetic forage cost for fish (see overview of planned experiments in Baxter *et al.* 2007), as well as on measured essential fatty acid composition. Herbivorous zooplankton species (e.g., cladocerans, calanoida) are expected to be of higher food quality because they graze on phytoplankton and are preferred prey item for fish , whereas predatory copepods (e.g., *Limnoithona spp.)* are expected to be a low nutritious food source. Understanding differences in patterns of influential zooplankton species and zooplankton forage quality for fish will be a first critical step to identify underlying mechanisms useful for management and restoration efforts.

(1b) **What are the long-term seasonal patterns in zooplankton species and functional groups?**

Rationale. The Delta ecosystem is highly variable at a seasonal scale, driven by environmental variables of freshwater flow rates, solar radiation, and temperature (Kimmerer 2004). Population dynamics of zooplankton in the system are strongly tight to the seasonality of temperature and resource availability and variation of these extrinsic factors can strongly modify the temporal population fluctuations in these organisms. Understanding long-term seasonal variability of zooplankton forage quantity and/or quality will be crucial for fish production, which exhibit different life histories and thus the timing of larval stages vary among species (summarized in Baxter *et al.* 2007). To better understand long-term seasonal variability in zooplankton, trends will be investigated at a seasonal basis for influential species and zooplankton aggregates (see above). Zooplankton functional groups will indicate to what extent species displacement affected the seasonal variability of food quality for fish.

Objective 2: **Identifying long-term interactions between primary producers and zooplankton**

Background – Primary production is the key energy source that sustains higher trophic levels and particularly in the Delta phytoplankton production fuels the pelagic food web (Jassby *et al.* 2002, Sobczak *et al.* 2002, Sobczak *et al.* 2005). Parallel decline in primary production, stocks of zooplankton and fish suggests that changes at the base of the food web and higher trophic levels are linked. Primary production rates in the Delta are inherently low because of light limitation (Jassby *et al.* 2002, Lopez *et al.* 2006) and growth and reproduction of crustacean zooplankton are limited by low phytoplankton biomass (Muller-Solger *et al.* 2002, Choi *et al.* 2005). The extent to which change in phytoplankton affect zooplankton production have however not been investigated in the Delta. Understanding this trophic linkages at large time scales and among stations will reveal whether bottom-up processes from primary producers to primary consumers are consistent or whether other mechanism such as species interactions or abiotic factors regulate zooplankton population dynamics.

Trends of primary producers measured as total phytoplankton biomass and gross primary productivity rates revealed spatial differences and an overall strong long-term declining trend (Jassby *et al.* 2002); for example production declined more then 40 % between 1975 and 1995. Current levels of average chlorophyll concentrations below 10 µg L^{-1} are below the earliest-recorded values (Jassby 2008). Feeding threshold values for most zooplankton organisms are within this range (Muller-Solger *et al.* 2002), thus declining trends may have critically affected zooplankton growth rates in this low-productivity system. A more recent analysis however indicated that phytoplankton biomass and production increased since the mid 1990s, particularly in the upper Delta region (but not in Suisun Bay), which is linked to reduced freshwater flow and increasing water clarity (Jassby 2008). Despite the recent recovery of primary production, primary and secondary pelagic consumers declined further and particularly fish species of concern declined drastically over the last recent years (Baxter *et al.* 2007). This suggests that while reduced primary production was likely the cause for the earlier decline, recent decline in zooplankton abundances can not be attributed to change in primary production.

Trophic ecology studies indicated that the diet composition varies among zooplankton species (Gifford *et al.* 2007). For example, the copepod *Acartia spp.* prey mainly on algal cells (diatoms and flagellates) and heterotrophic prey (ciliates and flagellates) in the size range >10 µm (Rollwagen Bollens & Penry 2003). Feeding experiments showed that the two copepod species, *E. affinis* and *C. ovata,* capitalize different plankton species (Mueller-Solger *et al.* 2006). *E. affinis* grazes indiscriminately on available algal and protozoan prey organisms, while *P. forbesi* more actively selects algal cells, particularly centric diatoms, and exerts a greater grazing pressure on its chosen prey. Experiments with the cyclopoid copepods like *L. tetraspina* showed that this abundant small species preys upon mixotrophic and hetertrophic ciliates, but rarely on diatoms (Bouley & Kimmerer 2006, Gifford *et al.* 2007). Because the importance of phytoplankton as a food source for zooplankton varies across species, temporal and spatial zooplankton changes may be independent of any change in primary producers and may explain why zooplankton did not respond to the recent recovery in phytoplankton.

This part of the proposed research aims to analyze long-term interactions of the phytoplankton-zooplankton trophic link, which will provide important information to what extent change in primary production and environmental variables affect primary consumers. This will be achieved by focusing on following questions:

***(2a)* How does phytoplankton and environmental variability affect zooplankton production at Delta-wide scale and appropriate sub-regions?**

Rationale. The plankton community in the Delta consists of different functional zooplankton species, including herbivores, omnivores, and predators, and thus it is expected that interactions between primary producers and primary consumers will differ among species. Besides food availability, zooplankton is also affected by abiotic factors such as freshwater flow rates and temperature. This part of the project will focus on understanding underlying processes for zooplankton variability. The response of zooplankton taxa and functional groups (see objective 1) to phytoplankton biomass, measured as chlorophyll concentration, and environmental variability will be analyzed across stations and for specific sub-regions identified for zooplankton in Objective 1 over the long-term and recent sampling record. Identification of regions with strong phytoplankton and zooplankton coherence will be indicative that bottom-up processes regulate primary consumer production, whereas weak coherence likely indicate that other factors limit zooplankton production. It is likely that zooplankton species displacement towards different functional groups that prey upon microzooplankton can be an underlying factor for the discrepancy. The outcome of this part will be informative to what extent change in primary producers and environmental variation affect zooplankton variability, and thus the energy transfer to upper trophic levels. Understanding differences and patterns across sub-regions or stations will be useful for restoration effort such as some regions may represent desirable restoration outcome with high trophic efficiency, while others can serve as baseline stations for restoration scenarios.

(2b) **Are seasonal patterns between primary producers and zooplankton consistent throughout the sampling record?**

Rationale. Copepods, the dominant zooplankton group and important food source for fish species of concerns in the Delta are relatively long-lived zooplankton species and duration of development varies between few weeks to one year. Successful life-cycle completion requires both synchrony with food availability and synchrony between development time and the time window of the available growing season (Cushing 1990, Edwards & Richardson 2004). Because estuarine habitats exhibit strong seasonal dynamics, it can be expected that the declining trend in zooplankton is linked to seasonal shifts in population dynamics resulting in a temporal disruption with their food resource. This part of the project will identify whether seasonal population dynamics of primary producers and influential zooplankton species and aggregates (see objective 1) were consistent over the sampling period or whether shifts in seasonality occurred. Seasonal shifts in zooplankton population dynamics may critical for fish development and result in a mismatch between food availability for fish species relative to fish growth performance.

Objective 3: **Identification of biotic interactions in the plankton community**

Background – Experimental food-web studies indicate that phytoplankton is a major food source for zooplankton. While phytoplankton production recovered during the last decade, zooplankton however did not respond to the recent increasing primary production trend (Cloern 2007, Jassby 2008). This discrepancy supports the notion that primary producers are a potential underlying cause for zooplankton decline until early 1990, but not afterwards. It is expected that the further decline of zooplankton populations is in part linked to change in algal food quality and/or palatability (Mueller-Solger *et al.* 2006), which depends on algal taxonomic composition (Brett & Muller-Navarra 1997) and cell morphology (Reynolds 2006). There is some evidence that phytoplankton community composition changed over the last decades in the Delta towards a shift of lower algal food-quality (Lehman 1996, Choi *et al.* 2005, Lehman *et al.* 2008). The proportion of diatoms decreased particularly during 1975 and 1989, caused by a decreasing trend in diatoms and an increasing trend in chlorophytes, cyanobacteria, and phytoflagellate abundances (Lehman 1996, Choi *et al.* 2005, Lehman *et al.* 2008). While there has been no discernable change in diatoms and phytoflagellates after 1990, cyanobacteria blooms of *Anacystis* and/or *Microcystis* have become an increasingly common phenomenon in the Delta in recent years (Lehman *et al.* 2008). Diatoms and cryptophytes are of high food quality for zooplankton because of their enrichment in essential fatty acids, whereas cyanobacteria have relatively low nutritional value (Brett & Muller-Navarra 1997). This indicates that the algal taxonomic composition is informative for the nutritional value for primary consumers, which is supported by experimental work indicating that algal species composition regulates zooplankton growth performance (Muller-Solger *et al.* 2002) and copepod production in the Delta (Mueller-Solger *et al.* 2006).

In addition to zooplankton displacement (see objective 2), change in food quality may be another reason why recent recovery of phytoplankton biomass (measured as chlorophyll concentration) did not translate into increasing zooplankton production. To fully understand the underlying processes that limit zooplankton production, algal food quality should be considered in trophic interactions. Such an approach however requires detailed species counts. Whereas the historical record for zooplankton is sufficient for such an approach, previous examination of the phytoplankton data set revealed limitation of its usage at the species level because the precision of the species values is overall low and small-sized cells have not been counted (Hymanson & Mueller-Solger 2001-2002). Analyses at the species level are therefore not recommended and phytoplankton biovolume can not be estimated based on algal cell counts. Nevertheless, the data are reliable at the class level and focusing on major phytoplankton groups will provide useful information for overall changes in food-quality for primary consumers.

Because all populations are embedded in a community, identifying dominant biotic interactions in the pelagic food web of the Delta and how they are affected by environmental variability will be important to understand underlying processes for plankton variability. At present, plankton biotic relationships are based on laboratory experimentation, observations, inferences from literature, and quantitative analyses between benthic grazers and phytoplankton biomass (Jassby *et al.* 2002, Kimmerer 2004). A cohesive analysis of the long-term dataset that includes different phytoplankton and zooplankton functional groups is still lacking in the Delta. While a detailed food-web modeling approach is too extensive within the 2-year funding period, basic interactions between phytoplankton functional groups and zooplankton trophic guilds, and environmental variables will be identified. If the available data are promising for food-web modeling, this will provide useful information for a more detailed analysis, which will be pursued if funding is continued. Within the 2-year funding period the following question will be addressed:

***(3a)* How do changes in plankton community composition relate to biotic interactions and environmental variation?**

Rationale. This part of the project will apply a quantitative multivariate analysis approach to investigate interactions between phytoplankton functional groups based on their nutritional value and zooplankton aggregates. In addition, changes in exogenous drivers, such as salinity, freshwater flow, and water temperature will be considered. Given that the quality of the phytoplankton data is sufficient for this analysis, the results will identify major species interactions and pathways through which abiotic variables may act on communities. Analyzing trophic food-web interactions at community-wide scale will be an important step in understanding the functioning of the pelagic communities and how they respond to environmental change.

2b. Approach and Plan of Work

Data source: Zooplankton, phytoplankton, chlorophyll and environmental data from 1975 to present will be provided by the California Departments of Water Resources and Fish and Game. Data for flow are available at http://www.iep.ca.gov/dayflow/index.html. The analysis will focus on long-term zooplankton monitoring stations in the Delta (around 14 stations, for map and station location see Mueller-Solger *et al.* 2006).

Approach for historical data analysis: A very large number of techniques are available for analyzing and understanding processes or mechanisms from long-term time series. Specific applications evolve from scientific understanding, the nature of the data as revealed through graphical exploration, the tools available to the analyst and trial-and-error. It is not possible to determine the exact course of an analysis beforehand. Specific previous time series analyses used in this estuary have been proven to be very successful. To address the proposed objectives some of these time series procedures and techniques applied in other aquatic systems will be used, while alternatives will be also explored in practice but will not be listed here.

Trend analysis – Monthly zooplankton will be used to identify long-term trends of the Delta's zooplankton species (Table 1). The temporal dynamics of the zooplankton will be characterized using single taxon abundances of influential community members and aggregate community properties (functional groups) based on biomass estimates to reflect the true contribution of individual species to total composition. The division into aggregate properties will be accomplished based on taxonomy (cladocerans, copepods, rotifers), knowledge of zooplankton ecology (herbivores, omnivores, predators), and food-quality for fish, based on nutritional value (for analysis see below). Zooplankton densities counts will be converted to biomass using established length-weight regressions from the Delta (available from A. Mueller-Solger and Bouley & Kimmerer 2006), or if not identified regressions will be measured (see below). Rotifer biomass will be estimated from literature sources (Hutchinson 1982, Walz 1995). If life stages are differentiated (see Table 1), biomass will be estimated for each stage to calculate total biomass.

For each zooplankton species and station, abundance/biomass will be binned by month using the mean to form a collection of monthly time series or by salinity intervals, which may reduce noise due to flow. Spatial coverage and length of the time series will be considered to which extent stations will be included in the analysis. The zooplankton data will be examined for groups of stations at which the corresponding species behaves similarly with respect to time. Representative stations will be selected for trend analysis, rather than repeating analyses for multiple stations that show the same variability pattern. Principal Component Analysis approach will be used as described by Jassby (2003). This approach is used often in meteorology and oceanography that cover a larger-spatial scale and has been used successfully in the Delta to identify seasonal patterns and sub-regions. The starting point will be a data matrix with columns representing monthly time series of zooplankton species. The principal components of the data matrix will be calculated, and a Monte Carlo technique used to determine the number of significant components. This reduced set of important principal components is then rotated using the PROMAX method to find a new set of components with so-called simple structure, in which individual stations are associated as much as possible with a single component. The end result is a small set of rotated components representing modes of variability. The temporal variability at any given station can be thought of as a combination of these modes, with the component coefficients representing the strength of each mode for that station. To the extent simple structure is achieved, the strength for a given station will be relatively large for only one mode.

The significance of trends will be determined by using the nonparametric Seasonal Kendall test with serial correlation correction (Hirsch & Slack 1984). The overall trend slope is computed as the median of all slopes between data pairs within the same season (no cross-season slopes contribute to the overall slope estimate), known as the Theil-Sen slope.

Because freshwater flow rates likely affect seasonal long-term changes of planktonic organisms (Bennett *et al.* 2002), the influence of flow rates has to be removed to increase the power of the test. Different approaches have to be considered for this correction, such as filtering of the flow time series. Long-term trends will be estimated after adjusting for total river inflow using locally weighted regression with a span of 0.5 and a locally linear fit (see Jassby 2008).

Seasonal variability – To identify long-term seasonal trends biomass will be binned by season [summer (Jun – Aug), fall (Sept – Nov), winter (Dec – Feb), spring (Mar – May)]. For influential zooplankton species and functional groups, spatial and temporal analysis will be applied as described above. If interesting long-term changes emerge from basic seasonal trend analysis, spectral analysis will be used to detect frequency components and potential shifts in seasonality over the period of record. This will be investigated using continuous wavelet transform (Torrence & Compo 1998), which quantifies both the amplitude of any periodic signals and how this amplitude varies with time. This analysis has been used successfully in biological communities to identify fluctuations in abundances (Bjørnstad *et al.* 1999, Jenouvrier *et al.* 2005, Nezlina & Li 2007, Vasseur & Gaedke 2007, Winder *et al.* in review). For zooplankton species of concern, i.e. species that show strong declining trends and/or are major food sources for larval fish, cross-wavelet power analysis (Grinsted *et al.* 2004) will be used to explore whether the coherence in the periodicity of the population dynamics and the periodicity of phytoplankton changed over the course of the study. This will find regions in time frequency space where two time series show high common power and will identify the time periods of strong covariation between primary producers and consumers.

Modeling phytoplankton (chlorophyll) and zooplankton interactions – Phytoplankton biomass will be calculated from chlorophyll *a* measurements and zooplankton densities will be converted to biomass (see above). Long-term biotic interactions will be first examines at the annual scale between chlorophyll *a* and zooplankton biomass aggregates (influential taxa, functional groups, total biomass). These interactions will be next examined at a monthly scale. If necessary, gaps in the time series will be imputed using a time-series modeling procedure that interpolates missing values based on the autocorrelation structure in the series (as described in Jassby 2005). In addition to phytoplankton biomass environmental variables (flow rates, temperature) will be included as predictor variables.

Temperature and flow rates affect zooplankton growth performance and needs to be considered in any analysis involving seasonal changes. Biotic interactions and the importance of the predictor variables for zooplankton will be explored using time series regression models. To account for serial correlation in the residual structure autoregressive models (ARIMA) will be applied (Box *et al.* 1994). Depending on the autocorrelation structure a first-order autoregressive model, moving average process and/or seasonal autoregressive term will be applied. The seasonal structure is expected to remove the long-term trend between plankton and flow rates. The removal of serial correlation will be examined using Durbin-Watson statistic and Ljung-Box *Q*-statistics for high-order serial correlation (Shumway & Stoffer 2000).

Food-web analysis – To evaluate how changes in the plankton community relate to biotic interactions and environmental change Multivariate Autoregressive models (MAR) (Ives 1995, Ives *et al.* 1999, Ives *et al.* 2003) will be applied. MAR modeling has been developed for analyzing long-term ecological data to quantify interactions among species and environmental drivers. The models partition effects of variables that are interrelated and temporally autocorrelated, features inherent to long-term observations. Autoregressive models explicitly use correlation between time steps to improve predictions. The usefulness of MAR modeling has been effectively demonstrated with plankton community data from the North Temperate Lakes Long-Term Ecological Research program (Beisner *et al.* 2003, Ives *et al.* 2003). MAR analysis may be interpreted as a set of multiple linear regressions solved simultaneously to achieve the greatest overall parsimony. The various interacting plankton species will be aggregated into functional categories based on annual averages. Algae will be categorized based on nutrition and palatability to grazers: diatoms, phytoflagellates (including dinoflagellates, chrysophytes, and cryptophytes), chlorophytes and cyanobacteria. The categorical variables will be related to exogenous drivers such as salinity, temperature, and freshwater flow. Zooplankton will be aggregated by trophic guilds (cladocerans, herbivore copepods, omnivore copepods) and benthic larvae stages. Results from this part of the proposed work will highlight strong species interactions and potential key players through the elimination of species interactions that are too weak to predict. The success of this goal will however largely depend on the quality of the phytoplankton dataset. If outcome of this approach are promising for Delta food-web analysis it will provide a useful tool on which future modeling can be based.

Laboratory analysis: Length- weight relationships will be measured for zooplankton species from which conversion factors have not been established in the Delta. Individual species and life stages representing different length will be dried and weighted. Zooplankton species that have unknown nutritional value, essential fatty acids will be measured. Samples will be taken during Delta cruises and zooplankton separated into species and life stages/length to be analyzed. Fatty acid analysis will be conducted at UC Davis (for preparation and analysis see http://stableisotopefacility.ucdavis.edu/).

Work plan – Schedule and timeline for this project are as follows:
Year 1: Zooplankton data analysis (Objective 1) and begin analysis of phyto- and zooplankton interactions (Objective 2). Zooplankton biomass estimation and fatty acid analysis.
Year 2: Finish analysis of Objective 2 and begin analyzing food-web interactions (Objective 3). Additional zooplankton fatty acid analysis.

2c. Output, anticipated Products and Benefits

The products and services humans derive from the Delta ecosystem depend largely on how food-web structure and carbon flow changes as the ecosystem faces increasing perturbations from human activities and climate change. To restore ecosystem productivity, central of the CALFED program mission, it is important to understand pelagic food-web structure and functioning, which will ultimately determine ecosystem health and productivity. The effort invested by the IEP to document such a long, detailed, and high-quality history of the Delta ecosystem yielded insights into various estuarine ecological processes. To this end however the analysis of existing plankton data is lagging behind and the data have not yet been utilized to its full extent (Hymanson & Mueller-Solger 2001-2002, Gaines *et al.* 2006). By capitalizing on the historical planktonic record of the Delta, analyzing, synthesizing and publishing this largely unstudied community dataset, the proposed research will achieve a major IEP goal (Mount 2008) and will promote greater understanding and innovation of the Bay-Delta ecosystem.

The historical database offers a unique opportunity to use statistical and modelling tools for determining the important factors underlying plankton dynamics. As such, the proposed research will produce new conceptualizations of the Delta's pelagic food-web dynamics including new insights on *i*) spatial and temporal zooplankton variability; *ii*) dynamics and impacts of phytoplankton variation on zooplankton production; *iii*) the interactive effects of planktonic organism and environmental change. The work outlined in this proposal will build on and extend the historical knowledge that describes the dynamics of the Delta. This will provide the opportunity to quantify the causes of pelagic production, to evaluate their consequences, and find preventative measures to enable the sustainable management and conservation of the estuarine ecosystems. This information will be relevant to ecosystem management and restoration effort and will interface with different ongoing planning activates and help build an understanding of the dynamics and variability of the Delta.

The project team is fully equipped to complement the proposed research. The research mentor (G. Schladow) has worked on physical aspects in the Delta system; all community mentors (J. Cloern, A. Jassby, W. Kimmerer) have a history of productive work in the Delta, are fully engaged in ongoing research project, and have extensively worked with historical data sets, statistical and modeling tools. The agency mentor (A. Mueller-Solger) will be the main collaborator at the State agency level, and is involved in monitoring design and thus has an excellent overview of the quality, availability, and accessibility of ecological data necessary for the proposed work and ongoing research in the Delta. M. Winder will greatly benefit from this fellowship, which will provide her the opportunity to expand her long-term ecological and quantitative skills to estuarine ecosystems. She will also profit from the collaborative work with the team mentors, who collectively have tremendous knowledge about the Delta ecosystem, ecological processes, and long-term ecological data analysis. The proposed work will complement and expand on research conducted by the research and community mentors and as such this research will be instructive for their ongoing research.

The outcome of this research addresses a priority research topic of the CALFED Science Program for the California Bay-Delta system: <u>Trends and Patterns of Habitats, Populations and System Response to a Changing Environment</u>. Because planktonic organisms are key component in the Delta's ecosystem to restore productivity, the proposed research will bridge the CALFED mission objective to improve and increase habitats and ecological functions in the Bay-Delta to support sustainable populations of diverse species.

The results of this research will be developed into:

Year 1: *i*) Annual progress report
- *ii*) Presentations at local (Bay-Delta) and national/international professional meetings
- *iii*) Draft of first manuscript

Year 2: *i*) Annual progress and final research report summarizing results and accomplishments
- *ii*) Presentations at local (Bay-Delta) and national/international professional meetings
- *iii*) Peer-reviewed scientific publications (at least two are anticipated)

In addition, analytical tools that will emerge as most suitable for the Delta database will be provided to agency staff, who will receive training through active participation in the analysis, and recommendations based on the analysis will be provided for the ongoing monitoring program.

Figure 1. Trend statistics of different zooplankton species in the Delta between 1972 and 2001. The trend for each taxon and station is plotted at the latitude (y-axis) and longitude (x-axis) for each station. Red downward pointing triangles = decreasing trends; green upward pointing triangles = increasing trends at p<-.05; grey circles = no significant trend. Vertical line denotes the Suisun-Delta boundary. (A. Jassby, unpublished results).

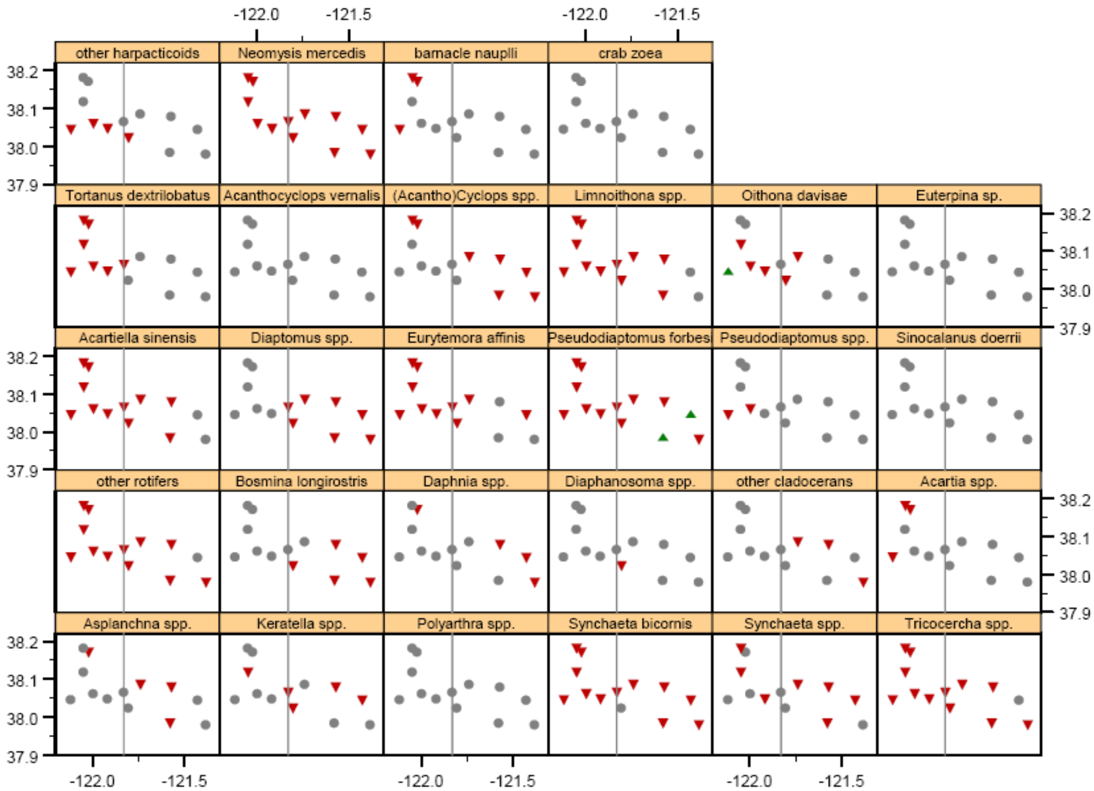

Table 1. Zooplankton species and life stages identified during in the long-term monitoring program of the Delta since 1975. In addition native vs. introduced copepod species are highlighted.

Species	Life stage	Native / Introduced	Species	Life stages
Copepoda			**Cladocera**	
Cyclopoida:			*Bosmina longirostris*	adults + juveniles
Acanthocyclops vernalis	adults	N	*Daphnia spp.*	adults + juveniles
Limnoithona spp.	adults/immatures	I	*Diaphanosoma spp.*	adults + juveniles
Oithona spp.	adults/immatures	N	*Ceriodaphnia spp.*	adults + juveniles
Oithona davisae	adults	I		
Calanoid copepod	immatures	N	**Rotifers**	
Oithona similis	adults	N	*Asplanchna spp.*	adults + juveniles
Calanoida:			*Keratella spp.*	adults + juveniles
Acartia spp.	adults/immatures	N	*Polyarthra spp.*	adults + juveniles
Acartiella sinensis	adults/immatures	I	*Synchaeta spp.*	adults + juveniles
Eurytemora spp.	adults/immatures/nauplia	I	*Synchaeta bicornis*	adults + juveniles
Euterpina acutifrons	adults	N	*barnacle nauplii*	adults + juveniles
Osphranticum labronectum	adults	I	*copepod nauplii*	adults + juveniles
Pseudodiaptomus forbesi	adults	I	*Trichocerca spp.*	adults + juveniles
Pseudodiaptomus marinus	adults	I	other Rotifers	adults + juveniles
Pseudodiaptomus spp.	adults/immatures/nauplia	N		
Sinocalanus doerrii	adults/immatures/nauplia	I		
Tortanus spp.	adults/immatures	I		
Calanoid copepod	immatures	N		
Diaptomidae		N		

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