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# Evaluating top-down, bottom-up, and environmental drivers of pelagic food web dynamics along an estuarine gradient

**Authors:** Tanya L. Rogers*[1], Samuel M. Bashevkin*†[2], Christina E. Burdi[3], Denise D. Colombano[4], Peter N. Dudley[1,5], Brian Mahardja[6], Lara Mitchell[7], Sarah Perry[8], Parsa Saffarinia[9]

**Affiliations:** [1]Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, [2]Delta Science Program, Delta Stewardship Council, [3]California Department of Fish and Wildlife, [4]Department of Environmental Science, Policy, and Management, University of California, Berkeley, [5]Fisheries Collaborative Program, Institute of Marine Sciences, University of California, Santa Cruz, [6]Bureau of Reclamation, [7]Lodi Fish and Wildlife Office, United States Fish and Wildlife Service, [8]California Department of Water Resources, [9]Department of Wildlife, Fish and Conservation Biology, University of California, Davis

*Equal contribution

†Corresponding author: sam.bashevkin@waterboards.ca.gov. Current affiliation: California State Water Resources Control Board

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## Abstract

Identification of the key biotic and abiotic drivers within food webs is important for understanding species abundance changes in ecosystems, particularly across ecotones where there may be strong variation in interaction strengths. Using structural equation models and four decades of integrated data from the San Francisco Estuary, we investigated the relative effects of top-down, bottom-up, and environmental drivers on multiple trophic levels of the pelagic food web along an estuarine salinity gradient and at both annual and monthly temporal resolutions. We found that interactions varied across the estuarine gradient, and that the detectability of different interactions depended on timescale. For example, for zooplankton and estuarine fishes, bottom-up effects appeared to be stronger in the freshwater upstream regions, while top-down effects were stronger in the brackish downstream regions. Some relationships (e.g., bottom-up effects of phytoplankton on zooplankton) were seen primarily at annual timescales, whereas others (e.g., temperature effects) were only observed at monthly timescales. We also found that the net effect of environmental drivers was similar to or greater than bottom-up and top-down effects for all food web components. These findings can help identify which trophic levels or environmental factors could be targeted by management actions to have the greatest impact on estuarine forage fishes, and the spatial and temporal scale at which responses might be observed. More broadly, this study highlights how environmental gradients can structure community interactions and how long-term datasets can be leveraged to generate insights across multiple scales.

## Introduction

Environmental gradients have long been useful for studying variation in trophic interactions, including the relative importance of top-down, bottom-up, and environmental influences on species distribution and abundance. Gradients in productivity (Power 1992) and stress (Menge and Sutherland 1987) have been of particular interest. For example, studies across elevational tidal gradients in rocky shore and salt marsh systems have provided many insights into how consumers, nutrients, and abiotic stressors regulate species abundances and community composition (Bakker et al. 2015). Experiments are common ways to test the strength of trophic and environmental controls across gradients (e.g., Alberti et al. 2010, McLaughlin and Zavaleta 2013), but this can be challenging in systems that are large and highly variable (such as pelagic ecosystems) or that involve rare or protected species. However, the increasing availability of integrated long-term, spatially-replicated, observational data opens new doors for examining food web dynamics using model-based approaches. By examining trophic and environmental interactions at different levels of spatial, temporal, and taxonomic resolution, it is possible to determine where and when different interactions manifest and the scales at which biotic or abiotic management interventions may (or may not) be detectable.

Estuaries are spatially and temporally variable transition zones between freshwater and marine environments that support diverse assemblages of benthic and pelagic algae, fishes, and invertebrates (Nelson et al. 2015). Species often respond to changes in hydroclimatic conditions (e.g., temperature, salinity), which can shift spatially across the ecotone and temporally over different timescales (Lauchlan and Nagelkerken 2020). Studies along estuarine gradients have examined how top-down, bottom-up, and environmental drivers affect benthic species (e.g., Leonard et al. 1998, Hauxwell et al. 1998, Kimbro et al. 2019) and select trophic levels of the pelagic food web (e.g., Hoover et al. 2006). Biotic and abiotic drivers have also been examined in pelagic communities in non-estuarine locations (Hampton et al. 2006, Lynam et al. 2017). For example, in the marine pelagic food web of the North Sea, commercial harvest of forage fishes alters plankton abundance via top-down effects, and sea surface temperatures drive plankton, fish, and seabird abundances via bottom-up and environmental effects (Lynam et al. 2017). However, because of the complexity of modeling spatiotemporally dynamic systems and the associated data requirements, relatively few studies have examined drivers of the full estuarine pelagic food web from phytoplankton to fishes, and how it varies across space and time. Understanding these influences in estuarine pelagic ecosystems is particularly important given the high prevalence of human impacts within certain estuaries (e.g., habitat and hydrologic alteration, introduced species, climate change), since these impacts can manifest as both bottom-up (McClelland et al. 1997) and top-down (Grimaldo et al. 2012) drivers.

Here we examine pelagic food web dynamics in the San Francisco Estuary, California, USA (hereafter, SF Estuary). Flow regulation (Monsen et al. 2007), loss of historical habitat (Nichols et al. 1986), and species introductions (Cohen and Carlton 1998) have altered the SF Estuary. The ecological impacts of these stressors have been monitored for decades (Tempel et al. 2021). Specifically, the introduction and proliferation of a small filter-feeding clam (*Potamocorbula amurensis*) has been implicated as one driver of the collapse of the pelagic food web, including phytoplankton (Jassby 2008), native zooplankton (Kimmerer and Orsi 1996), and forage fishes (e.g., Delta Smelt, *Hypomesus transpacificus*; Longfin Smelt, *Spirinchus thaleichthys*; Mac Nally et al. 2010). Studies using multivariate models have investigated biological and environmental drivers of this food web and found that the primary proximate drivers were salinity and water clarity (Mac Nally et al. 2010, Feyrer et al. 2015). We expand on these prior studies by examining drivers of multiple trophic levels across more and finer spatial, temporal, and taxonomic scales. Using a single modeling framework and more than a decade's worth of additional data, we integrate multiple data sources, sampling gear types, and species interactions.

We asked two overarching questions: (1) what are the relative effects of top-down, bottom-up, and environmental drivers on pelagic food web dynamics in the SF Estuary, and (2) how do these effects vary over spatial scales (the estuarine gradient) and temporal scales (monthly to annual)? To address these questions, we first developed a conceptual model of hypothesized food web interactions (among phytoplankton, clams, zooplankton, and forage fishes) and environmental drivers (flow/salinity, temperature, water clarity, nutrients) based on previous studies in this system. We then quantified support for these interactions using structural equation models (SEMs) fit to publicly available long-term monitoring data (**Table 1**) collected along the estuarine salinity gradient over four decades (1980-2020). We compared results from models at different spatial, temporal, and taxonomic resolutions to assess interactions within and among trophic levels. Finally, we summarized the net effects of different interaction types in the high temporal resolution models.

## Methods

### ***Study area***

The SF Estuary is California's largest estuary, stretching from San Francisco Bay to the tidal freshwater Sacramento-San Joaquin Delta. Large pumping facilities in the southern Delta export freshwater towards southern California, while the rest flows downstream towards Suisun Bay, San Pablo Bay, and eventually the Pacific Ocean (**Fig. 1**). The Delta is managed to remain fresh year-round and only experiences salinity intrusion during extreme drought years, whereas San Pablo and Suisun Bays have more variable salinities. The SF Estuary has a Mediterranean climate with a wet winter-spring and a dry summer-fall, resulting in considerable intra-annual variability in inflow, salinity, and temperature. California also experiences high interannual variability in precipitation, leading to swings between droughts to floods. Due to the system's complexity and its central role in water supply for the state of California, there are over 20 long-term monitoring programs conducted by government agencies and universities, mostly started between the 1950s and 1990s (https://iep.ca.gov/Data/IEP-Survey-Data).

### *Data processing*

We compiled data (Mitchell et al. 2023) from eight long-term monitoring programs that sample different components of the food web (**Table 1**). We obtained data on chlorophyll-a (a proxy for phytoplankton), six aggregate categories of zooplankton (cladocerans, herbivorous copepods, predatory copepods, mysids, amphipods, and rotifers; specific species given in **Appendix S1: Table S1**), two clam species (*Potamocorbula amurensis* and *Corbicula fluminea*, hereafter *Potamocorbula* and *Corbicula*), and an aggregate of estuarine fishes from each of three different surveys (Fall Midwater Trawl, FMWT; Summer Townet, STN; San Francisco Bay Study Midwater Trawl, BSMT). The fishes included in this aggregation were five commonly caught, planktivorous, freshwater-brackish fish species of high management interest: Delta Smelt, Longfin Smelt, Threadfin Shad (*Dorosoma petenense*), juvenile American Shad (*Alosa sapidissima*), and age-0 Striped Bass (*Morone saxatilis*). We also assembled data on potential competitors and predators of the estuarine forage fishes, specifically planktivorous marine fishes (aggregate of Northern Anchovy [*Engraulis mordax*] and Pacific Herring [*Clupea pallasii*], competitors), Mississippi Silverside (*Menidia audens*, competitor), age-1+ Striped Bass (predator), and fishes from the centrarchid family (predators, **Appendix S1: Table S1**). We used biomass per unit effort (BPUE) for all biological variables except the clams, for which only count per unit effort was available for the full timeseries. We also obtained data on dissolved inorganic nitrogen (DIN) and three environmental drivers: temperature, flow, and turbidity.

Phosphorous was considered but excluded because it is not limiting in the system (Cloern et al. 2020), and salinity was considered but excluded as it is highly correlated with flow in this system. We ensured the methods and units were comparable for any variables that were aggregated. Further details are provided in **Appendix S1: Supplemental Methods**.

Each variable in each source dataset was summarized into annual, annual-regional, and monthly-regional averages (**Appendix S1: Figs S1-5, Table S2**), allowing for models with different spatial and temporal resolutions. Both the annual and annual-regional datasets spanned 40 years (1980-2020). The monthly-regional dataset spanned 24 years (1997-2020), as monthly resolution data were only available over this time period. We only calculated averages from continuously monitored sampling stations (**Appendix S1: Table S3)**. For both annual- and monthly-regional datasets, the SF Estuary was divided into four regions representing different salinity and hydrodynamic habitat types within the SF Estuary: San Pablo (San Pablo Bay; brackish), Suisun (Suisun Bay; brackish), Sacramento (lower Sacramento River; freshwater), and San Joaquin (lower San Joaquin River; freshwater) (**Fig. 1**). Due to limited sampling in San Pablo before the mid-1990s, this region was only included for the monthly-regional dataset.

### ***Analysis***

We evaluated relationships among the food web components and environmental drivers using structural equation models (SEMs), a common tool for investigating dominant pathways in ecological networks including food webs (Grace et al. 2010). We first developed a conceptual model of the hypothesized direct relationships between all variables for which we had data (**Fig. 2**). These relationships reflected known ecological interactions and were based on existing literature and our knowledge of the system (**Appendix S1: Table S4**). From the conceptual model, we developed simplified models for each level of spatiotemporal resolution (annual,

annual-regional, and monthly-regional) that had a corresponding dataset (**Appendix S1: Table S5**). These simplifications, including data aggregation, were required in order to have models that were feasible (given the quantity of available data) and interpretable. Regional models at both time scales were fit separately to each region. Species were omitted from models of particular regions if they were rare or not sampled in that region.

The annual and annual-regional models had the same structure and focused on the relative importance of environmental drivers and food supply for estuarine fishes. For these models, we computed two aggregate zooplankton variables representing two trophic levels: herbivorous zooplankton (cladocerans + herbivorous copepods + rotifers) and predatory zooplankton (predatory copepods + mysids). Amphipods were not included in these aggregates because the units of BPUE were not equivalent. Estuarine fishes were modeled as a latent variable manifested by three survey datasets (BSMT, FMWT, STN). Environmental drivers and clams were included as exogenous predictors. Contemporaneous values were used for all relationships because of the sub-annual life histories of plankton, although because of this we could not evaluate bidirectional effects (bottom-up and top-down) simultaneously, as was possible in the monthly models using time lags (see below). Thus, trophic interactions were assumed to be bottom-up (except for clam effects on plankton) to facilitate evaluation of food supply effects on estuarine fishes.

For the monthly-regional data, we employed three submodels with different sets of focal (endogenous) response variables, which allowed us to explore more detailed interactions between adjacent trophic levels. We had an ‘upper trophic level,’ (response variables: estuarine fishes from BSMT, herbivorous zooplankton, predatory zooplankton), a ‘lower trophic level’ model (DIN, phytoplankton, clams), and a model of individual zooplankton groups. All models used 1-month lagged values for the biological predictors: a response variable was influenced by lower trophic levels, higher trophic levels, and itself at a 1-month lag, thus allowing us to account for autocorrelation/self-regulation, bottom-up effects, and top-down effects while maintaining a recursive model structure. For the upper and lower trophic level models, we computed the total effect size of each interaction type (self-regulation, bottom-up, top-down, environmental, nutrient cycling) for each response variable as the square root of the sum of squared path coefficients corresponding to each interaction type. Since the monthly data displayed high seasonality, we removed the seasonal trend from each variable by subtracting the mean monthly value from each timepoint. Models were fit to the resulting seasonal anomalies.

All variables were log transformed (except temperature, turbidity, and clam densities) and scaled to mean 0 and unit variance. We ensured that all final models were plausible given the data (chi-squared $p>0.05$) and our understanding of the system. SEM models were fit using the lavaan package (Rosseel 2012) in R version 4.0.2 (R Core Team 2020). Further analytical details can be found in Appendix S1: **Supplemental Methods**. We note that these models had a large number of parameters relative to data (Wolf et al. 2013). Thus, a non-significant result does not mean the relationship is absent or unimportant, but simply that we did not find support for it in this analysis.

## Results

### *Annual and annual-regional models*

We found consistent positive effects of zooplankton BPUE (either herbivorous or predatory) on estuarine fishes in all regions (standardized path coefficient range: 0.15 to 0.61). These effects were significant in the whole estuary and in the freshwater Sacramento and San Joaquin (**Fig. 3**). Significant trophic links between chl-a and herbivorous zooplankton, and between herbivorous and predatory zooplankton were found in the whole estuary, Suisun, and San Joaquin (0.28 to 0.61). Thus, the whole estuary and San Joaquin had bottom-up links extending completely from phytoplankton to zooplankton to fishes. *Potamocorbula* clams had negative effects on estuarine fishes and herbivorous zooplankton in the whole estuary (-0.32 and -0.31 respectively) and the brackish Suisun (-0.33 and -0.35). In contrast, *Corbicula* clams showed a positive relationship with zooplankton and phytoplankton in the freshwater Sacramento and San Joaquin (0.28 to 0.45).

Turbidity had consistent positive effects on estuarine fishes in all regions (0.26 to 0.79), on herbivorous zooplankton in Sacramento (0.45), and on phytoplankton in San Joaquin (0.37), but a negative effect on herbivorous zooplankton in Suisun (-0.28). Flow had a negative effect on predatory zooplankton in all regions (-0.20 to -0.38) except San Joaquin. Temperature had no significant effects on any variables.

### ***Monthly-regional models***

In the monthly models, most response variables had relatively low $R^2$ values (typically <0.5), with significant regional variability. All response variables except estuarine fishes and herbivorous copepods in Sacramento and rotifers in San Joaquin showed a significant positive relationship with past (1-month lagged) abundance.

#### *Upper trophic level model*

For zooplankton and estuarine fishes, bottom-up effects appeared to be stronger in the freshwater upstream regions (Sacramento and San Joaquin) while top-down effects appeared stronger in the brackish downstream regions (Suisun and San Pablo; **Figs. 4, 5**). For herbivorous zooplankton, total bottom-up effects were significant in San Joaquin, while top-down effects were significant in San Pablo and Suisun. For predatory zooplankton, bottom-up effects were significant in Suisun, Sacramento, and San Joaquin, while total top-down effects were not significant in any region. For estuarine fishes, bottom-up effects were significant in San Pablo, Sacramento, and San Joaquin (range 0.13 to 0.14). Total top-down effects on fishes were only significant in Suisun and Sacramento, although the effect of Striped Bass was positive in Suisun (**Fig. 4c**). *Potamocorbula* clams had negative effects on herbivorous zooplankton in Suisun (-0.22) and San Pablo (-0.21), while *Corbicula* clams had no significant effects.

Environmental drivers were significant for nearly all response variables (**Fig. 5**). The net effect of environmental drivers was typically on par with or greater than bottom-up and top-down effects (**Fig. S6a**). Consistent with the annual models, turbidity had a positive effect on fishes in San Pablo, Suisun, and San Joaquin (0.21 to 0.23; **Fig. 4**). In contrast to the annual models, flow had a negative effect on fishes in Suisun (-0.21) and Sacramento (-0.44). The effect of flow on zooplankton varied by trophic level, with negative effects on predatory zooplankton in Sacramento (-0.44) and San Joaquin (-0.13) and positive effects on herbivorous zooplankton in Suisun (0.18), Sacramento (0.24), and San Joaquin (0.19).

*Lower trophic level model*

Bottom-up effects on clams and phytoplankton were largely absent, and the only observed effects of lower trophic levels on higher trophic levels were negative (DIN on phytoplankton in Sacramento [-0.13] and predatory zooplankton on clams in San Pablo [-0.16], **Fig. 6**). Total top-down effects on phytoplankton were only significant in Sacramento. $R^2$ values for phytoplankton were very low in all regions. For DIN, top-down effects of phytoplankton were significant and negative in all regions (-0.13 to -0.20). This effect was not lagged because a lag was not supported by the data.

Total environmental drivers were significant for all variables except phytoplankton in

Suisun and San Joaquin (**Fig. 5**). Total environmental effects exceeded total top-down effects for DIN in all regions (**Fig. S6b**). Flow had a negative effect on DIN in all regions except San Joaquin, and effects increased in strength from San Pablo to Suisun to Sacramento (-0.18 to -0.46). One case of nutrient cycling was detected in San Joaquin, where upper trophic levels (predatory zooplankton) had a positive effect on DIN (0.12).

### *Zooplankton model*

Results from the individual zooplankton model were largely consistent with the upper trophic level model (**Fig. S7**). Bottom-up effects of phytoplankton on zooplankton were most prevalent in the freshwater San Joaquin and absent from the brackish San Pablo. Estuarine fishes had negative top-down effects on amphipods and rotifers in Suisun and on herbivorous copepods in San Joaquin. Herbivorous copepods were affected negatively by *Potamocorbula* clams in San Pablo (-0.16) and Suisun (-0.17), and positively by *Corbicula* clams in Sacramento (0.13) and San Joaquin (0.12). Interactions among zooplankton groups were most common in Suisun, which also had the highest density of significant interactions. Environmental effects were regionally and taxonomically variable with mixed positive and negative effects of flow and turbidity but predominantly positive temperature effects.

## Discussion

In this study, we used four decades of integrated biological and environmental data to investigate the relative effects of top-down, bottom-up, and environmental drivers on pelagic food web dynamics in the SF Estuary and how these effects vary over spatial and temporal scales. We found that interactions varied across the estuarine gradient, that different interactions were detectable on monthly and annual timescales, and that the net effects of biotic and abiotic drivers were comparable in magnitude for all components of the food web.

Theoretical and empirical studies have found that greater diversity (Srivastava et al. 2009, Griffin et al. 2013, Ye et al. 2013) and lower productivity (Oksanen et al. 1981, van de Koppel et al. 1996, Chase et al. 2000) can each result in stronger top-down effects. This is consistent with our findings: greater top-down effects were seen in the brackish mixing region of the estuary (Suisun), which had a greater diversity of consumers and lower productivity than the freshwater regions. Suisun had the greatest number of interactions in the individual zooplankton model, along with higher zooplankton diversity and abundance. Brackish regions also contained top-down effects from the invasive clam *Potamocorbula*, which has been implicated by other studies in plankton declines (Kimmerer 2002) and is known to have a much higher grazing rate than the more freshwater *Corbicula* (Foe and Knight 1986, Cole et al. 1992). In estuaries, mixing zones such as our Suisun region are often characterized by regional productivity maxima due to the occurrence of the estuarine turbidity maximum zone (Simenstad et al. 1990), an area where detrital particles and organisms are concentrated. However, this estuarine turbidity maximum zone only appears intermittently in the SF Estuary (Monismith et al. 1996, but see Young et al. 2021 for a localized turbidity maximum upstream of our study region), and since the *Potamocorbula* clam invasion, the mixing zone has been a net productivity sink receiving subsidies from more productive areas up and downstream (Brown et al. 2016). Thus, the pattern we document (greater top-down forces in the brackish downstream regions and greater bottom-up forces in the freshwater upstream regions) may be in part due to impacts of the co-occurring productivity and diversity gradients.

Declining effects of flow on DIN from Sacramento to San Pablo potentially reflect nutrient export processes and flow-related dilution of wastewater discharge, which is a major source of nitrogen upstream of the Sacramento region (Jassby 2008). Although a study of 14

Australian estuaries found that higher DIN can lead to increases in macroalgae, vegetation, and phytoplankton chlorophyll (Woodland et al. 2015), we did not detect bottom-up effects of DIN on phytoplankton**.** This is likely because the SF estuary is paradoxically nutrient rich but productivity poor due to its high turbidity (Dahm et al. 2016). The Sacramento Wastewater Treatment Plant that provides much of the nitrogen was recently upgraded to reduce total nitrogen loading and almost eliminate the proportion discharged as ammonia (State Water Resources Control Board 2023). These changes may alter the patterns we detected and will provide an opportunity to investigate ecosystem-wide consequences of estuarine nitrogen loading (e.g., Woodland et al. 2015).

Difference in the rate of biotic and abiotic processes likely explains why different interactions occurred and were detectable on different timescales. For instance, negative top-down effects of phytoplankton on DIN were rapid (no lag), likely due to rapid nutrient uptake during phytoplankton blooms (Peterson et al. 1985). The effects of flow on estuarine fishes varied with timescale, likely reflecting different population processes: monthly flow effects reflect fish movement and distributional shifts within the estuary, whereas annual effects reflect interannual changes in population size. Temperature effects were visible on monthly but not annual timescales likely due to greater intra-annual variability, whereas bottom-up effects were stronger/more apparent on the annual as opposed to monthly timescale. Knowledge of these timescales matters as inferences drawn about the relevance of certain drivers will be conditional on the timescale examined. Additionally, different responses can be expected on different timescales following a manipulation, disturbance, or management action.

Past studies on zooplankton and forage fishes in estuaries (including the SF estuary) have found stronger influences of abiotic than biotic drivers (Thomson et al. 2010, Rollwagen-Bollens et al. 2020, Wasserman et al. 2022). However, we found net biotic and abiotic effects to be of comparable magnitude. We also found that driver strength was variable by region and time scale, agreeing with prior studies that have found variability in the relative importance of biotic and abiotic drivers with spatiotemporal context (Guinder et al. 2017, Smits et al. 2023). From a management perspective, the relative importance of abiotic drivers is important because environmental factors (namely flow and turbidity) can often be manipulated directly, e.g., through freshwater flow manipulation (Hemraj et al. 2017, Sommer 2020). For increasing the abundance of estuarine fishes and their food supply, this can be easier to implement than biotic interventions such as predator removal.

With regard to the SF Estuary specifically, our analysis incorporated 12 additional years of data than the last multivariate pelagic food web analysis in this system (Mac Nally et al. 2010). While our models are not directly comparable due to different spatiotemporal scales, we were able to identify some food web relationships not present in Mac Nally et al. (2010): the bottom-up effects of chlorophyll on estuarine fishes via zooplankton, trophic relationships among zooplankton guilds, and regionally-dependent effects of flow on multiple trophic levels. Overall, our results support the importance of flow and turbidity in estuaries (Cloern 1987) and their mixing zones (Nelson et al. 2015, Wang et al. 2021), as well as food supply as a critical management objective in the SF Estuary. The **Supplemental Discussion** (Appendix S1) contains more discussion of the model pathways in relation to prior research in the SF Estuary.

Our study was limited by lack of regular, long-term monitoring data on several important food web components. For instance, we used chlorophyll as a coarse proxy for phytoplankton abundance since we lacked high-quality, long-term phytoplankton data. Although chlorophyll was often a significant driver of zooplankton, chlorophyll itself was poorly explained by the predictors in our models. Additional variables such as residence time or light availability (Kimmerer 2002) might be influential. We also lacked data on large-bodied piscivorous fishes, which can exert strong top-down effects (Carpenter et al. 1985); microplankton (e.g., ciliates and bacteria), which are often consumed by 'herbivorous' zooplankton (Gifford et al. 2007); submersed and emergent aquatic vegetation, which can contribute substantially to the pelagic trophic pathway (Young et al. 2020); contaminants (e.g., herbicides, pesticides), which can have considerable impacts on food webs and are a known issue in the SF Estuary (Fong et al. 2016); and entrainment of phytoplankton, zooplankton, and fishes in the water export pumps. These data gaps highlight potential priorities for future monitoring.

In some cases, the models suggested paths that were unexpected, given our conceptual model. For instance, some of the paths added to properly reflect covariance in the data appeared to 'skip' trophic levels (e.g., phytoplankton had significant effects on predatory taxa). Other paths had opposite signs as expected from a priori knowledge (e.g., positive effects of age 1+ striped bass on estuarine fishes in Suisun). Possible explanations for this include missing shared drivers and/or indirect effects. Indirect effects can appear direct if integrated over a long enough timestep (i.e., monthly effects are not 'instantaneous,' but integrated over a month). The linear additive structure of SEMs also does not allow for interactions among predictors, nonlinear effects, or time-varying effects, limiting our ability to resolve complex food web interactions (e.g., how biotic interactions vary with environmental conditions within a region). Some of the inconsistent linear effects we observed may indicate higher-order predator-prey interactions such as prey-switching behavior, which SEMs would not be able to account for. For instance, we found effects of fish on zooplankton in some regions, with the specific region(s) varying depending on whether trophic level aggregates or individual zooplankton groups were used.

Future work in the SF Estuary might use our food web model and integrated dataset (Mitchell et al. 2023) as the groundwork for predictive models that can inform management (Adams et al. 2020, Munch et al. 2023). The recovery of estuarine forage fishes is a key objective, and the use of predictors which are directly manipulable could produce specific predictions for the food web in response to certain management actions. However, as many abiotic drivers are collinear (e.g., nutrients), further studies would be needed to disentangle their effects. Improvements to the model could include the use of variable (rather than uniform) inter- and intra-specific time lags for each component, accounting for differences in the intrinsic timescales of movement, growth, and reproduction among species. Additional analyses might also consider using salinity zones rather than fixed geographic regions to account for transportation of the pelagic community, reduce covariance between salinity and flow, and increase comparability to other estuarine systems.

More broadly, our approach of integrating long-term datasets to identify biotic and abiotic drivers across trophic levels, including the spatial and temporal scales of these interactions, is applicable to a wide range of systems. Species invasions, changes in land and water use, climate change, and other anthropogenic impacts will affect physical drivers and food web interactions across the globe. The development and efficacy of management actions will likely hinge on the understanding of ecosystem dynamics through their various drivers. This study serves as an example of how we can leverage natural variability to address longstanding questions into the relationships among productivity, diversity, environmental context, and trophic control within ecosystems.

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## Tables

**Table 1.** Variables and data sources

| Variables | Data source | Citation |
|---|---|---|
| Zooplankton (cladocerans, herbivorous copepods, mysids, predatory copepods, rotifers) | Environmental Monitoring Program (EMP Zooplankton) | (Barros 2021) |
| Benthic invertebrates (clams, amphipods) | Environmental Monitoring Program (EMP Benthic) | (Wells and Interagency Ecological Program 2021) |
| Fish (estuarine fishes, marine fishes, age 1+ striped bass) | San Francisco Bay Study Midwater Trawl (BSMT) | https://wildlife.ca.gov/Conservation/Delta/Bay-Study |
| Fish (estuarine fishes) | Fall Midwater Trawl Survey (FMWT) | https://dfg.ca.gov/delta/projects.asp?ProjectID=FMWT |
| | Summer Townet Survey (STN) | https://wildlife.ca.gov/Conservation/Delta/Townet-Survey |
| Fish (Mississippi Silverside, centrarchid species) | Delta Juvenile Fish Monitoring Program (DJFMP) | (Interagency Ecological Program et al. 2021b) |
| Chlorophyll-*a*, Temperature, Secchi depth, Nutrients | Environmental Monitoring Program (EMP Water Quality) | (Interagency Ecological Program et al. 2021a) |
| Flow | Dayflow, California Department of Water Resources | https://data.cnra.ca.gov/dataset/dayflow |

## Figure captions

**Fig. 1**. Map of the SF Estuary, California, USA with region (San Pablo, Suisun, Sacramento, San Joaquin) boundaries and survey stations used in (a) annual and annual-regional analyses and (b) monthly-regional analyses. The Sacramento and San Joaquin regions are contained within the primarily freshwater Sacramento-San Joaquin Delta, while Suisun and San Pablo are more dynamic in salinity and remain largely brackish to marine. For survey acronyms, see Table 1.

**Fig. 2.** Conceptual model of hypothesized relationships between all variables. Direct consumption arrows point in the direction of energy flow.

**Fig. 3.** Path diagrams for annual and annual-regional SEMs. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate coefficients not significantly different from 0. Arrow thickness is proportional to the magnitude of the standardized path coefficient. Latent variables are represented by ovals. Numbers next to each variable are associated $R^2$ values. Colors of variables match the colors in the conceptual model.

**Fig. 4.** Path diagrams for monthly-regional SEMs using upper trophic level aggregates. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate coefficients not significantly different from 0. Arrow thickness is proportional to the magnitude of the standardized path coefficient. Numbers next to each variable are associated $R^2$ values. Colors of variables match the colors in the conceptual model.

**Fig. 5.** Summary of total effect sizes for upper trophic level and lower trophic level monthly-regional SEMs. Colors of variables match the colors in the conceptual model. Filled squares = total effect significant ($p<0.05$), gray squares = total effect not significant, blank = not tested. For

values of total effect sizes, see **Fig. S6**.

**Fig. 6.** Path diagrams for monthly-regional SEMs using lower trophic level aggregates. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate coefficients not significantly different from 0. Arrow thickness is proportional to the magnitude of the standardized path coefficient. Numbers next to each variable are associated $R^2$ values. Colors of variables match the colors in the conceptual model.

# Figures

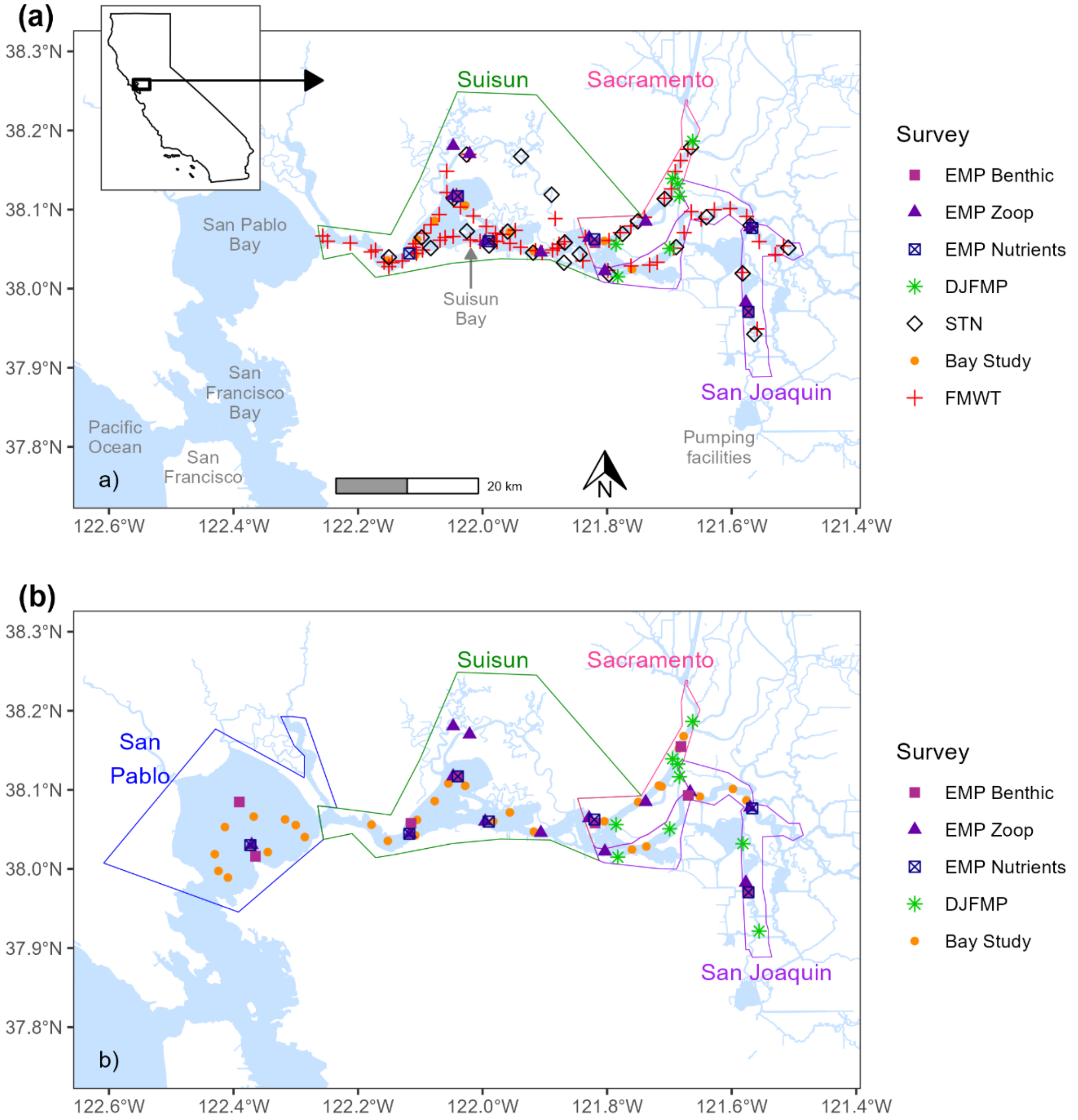


**Figure 1**

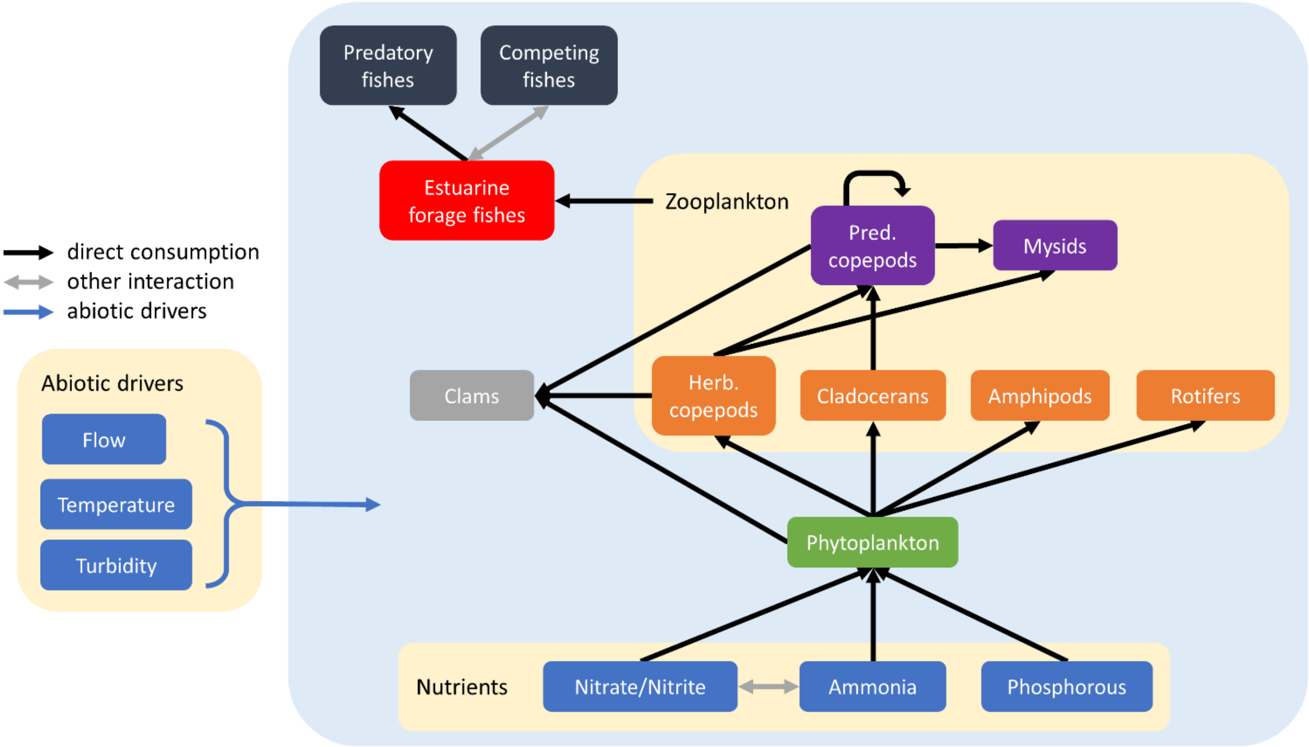

Predatory fishes
Competing fishes
Estuarine forage fishes
Zooplankton
Pred. copepods
Mysids
direct consumption
other interaction
abiotic drivers
Abiotic drivers
Flow
Temperature
Turbidity
Clams
Herb. copepods
Cladocerans
Amphipods
Rotifers
Phytoplankton
Nutrients
Nitrate/Nitrite
Ammonia
Phosphorous

**Figure 2.**

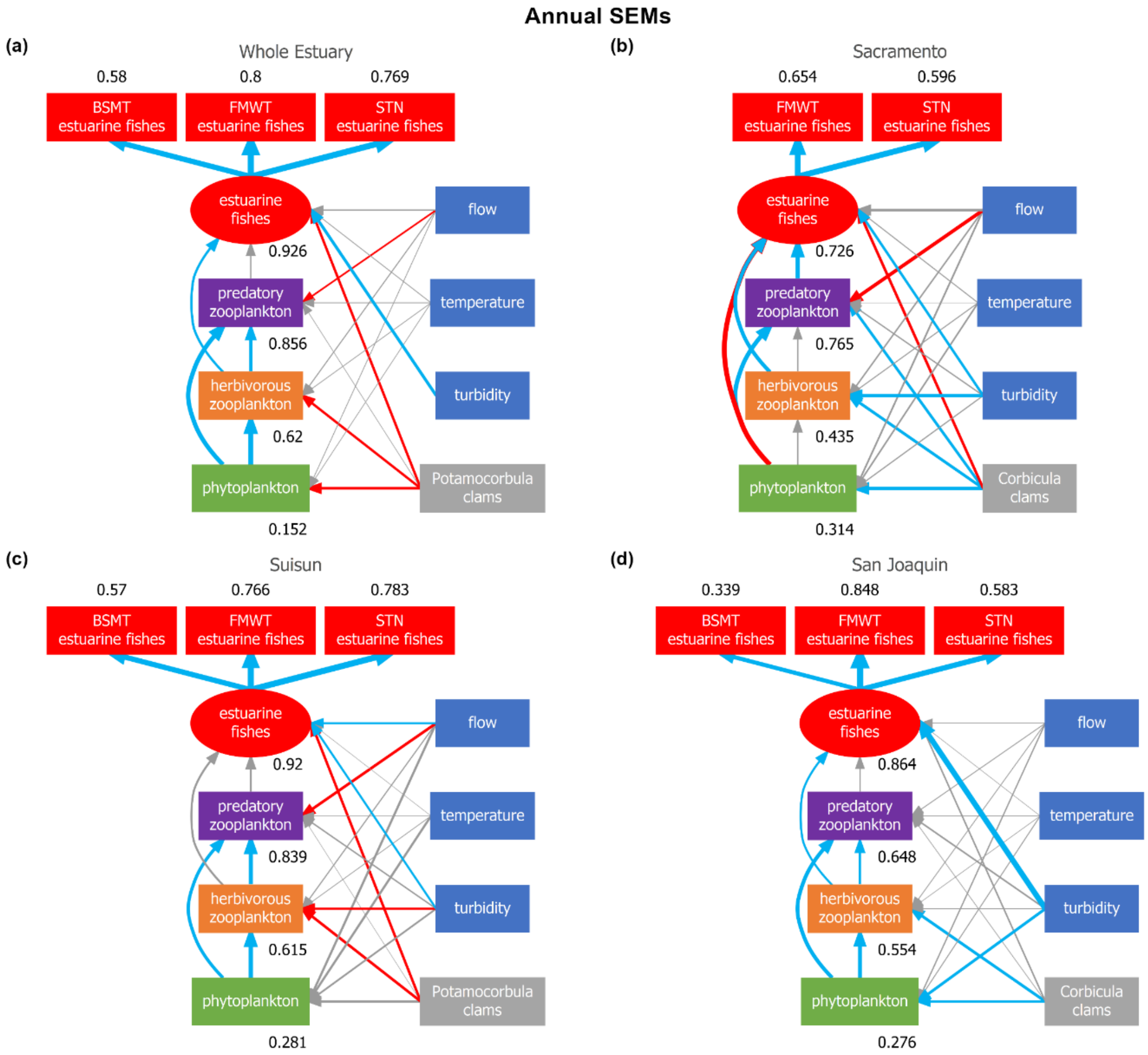

Annual SEMs
(a)
Whole Estuary
0.58
0.8
0.769
BSMT estuarine fishes
FMWT estuarine fishes
STN estuarine fishes
estuarine fishes
0.926
predatory zooplankton
0.856
herbivorous zooplankton
0.62
phytoplankton
0.152
flow
temperature
turbidity
Potamocorbula clams
(b)
Sacramento
0.654
0.596
FMWT estuarine fishes
STN estuarine fishes
estuarine fishes
0.726
predatory zooplankton
0.765
herbivorous zooplankton
0.435
phytoplankton
0.314
flow
temperature
turbidity
Corbicula clams
(c)
Suisun
0.57
0.766
0.783
BSMT estuarine fishes
FMWT estuarine fishes
STN estuarine fishes
estuarine fishes
0.92
predatory zooplankton
0.839
herbivorous zooplankton
0.615
phytoplankton
0.281
flow
temperature
turbidity
Potamocorbula clams
(d)
San Joaquin
0.339
0.848
0.583
BSMT estuarine fishes
FMWT estuarine fishes
STN estuarine fishes
estuarine fishes
0.864
predatory zooplankton
0.648
herbivorous zooplankton
0.554
phytoplankton
0.276
flow
temperature
turbidity
Corbicula clams

**Figure 3.**

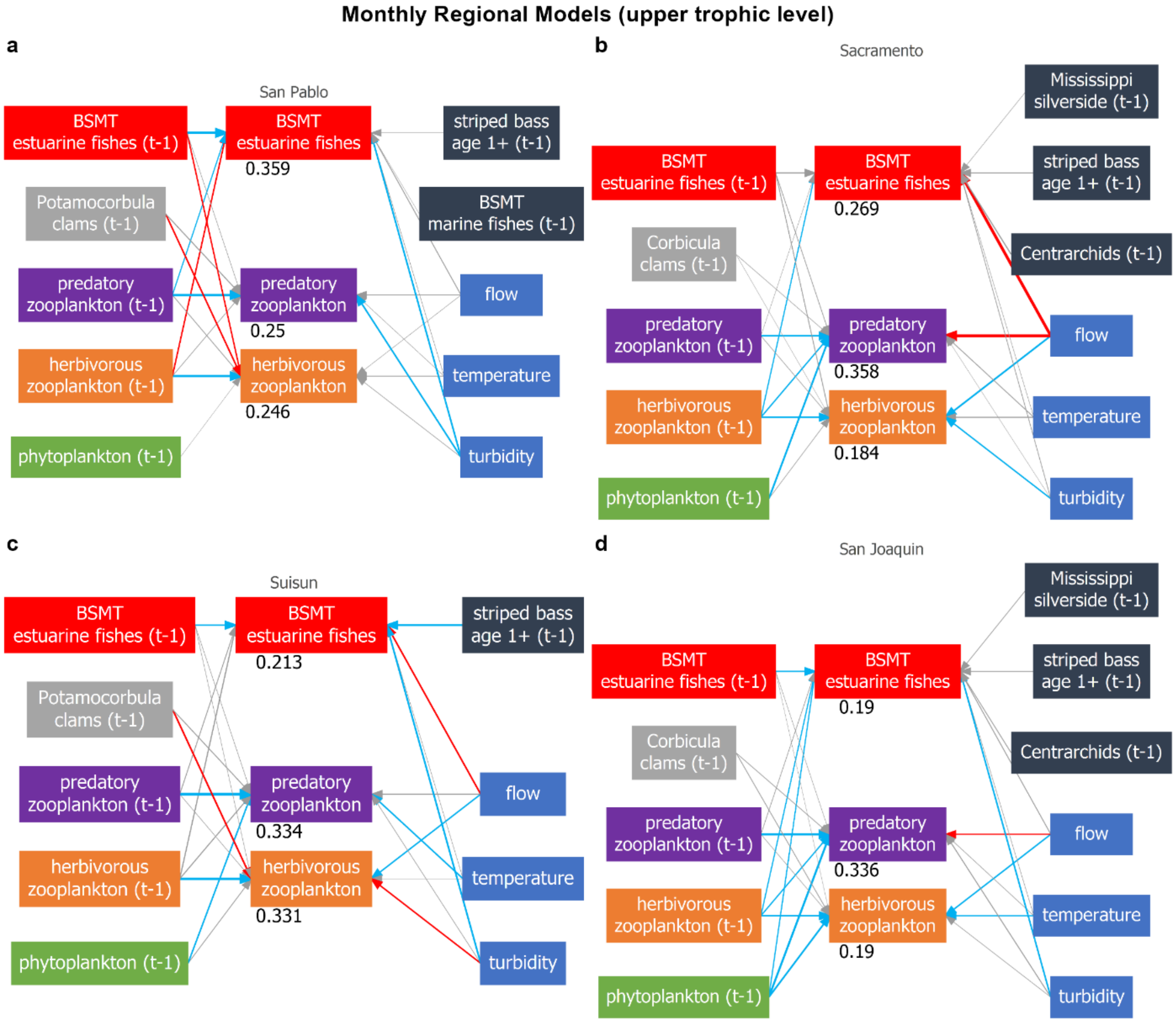

Monthly Regional Models (upper trophic level)
a
San Pablo
BSMT estuarine fishes (t-1)
BSMT estuarine fishes
0.359
striped bass age 1+ (t-1)
Potamocorbula clams (t-1)
BSMT marine fishes (t-1)
predatory zooplankton (t-1)
predatory zooplankton
0.25
flow
herbivorous zooplankton (t-1)
herbivorous zooplankton
0.246
temperature
phytoplankton (t-1)
turbidity
b
Sacramento
Mississippi silverside (t-1)
BSMT estuarine fishes (t-1)
BSMT estuarine fishes
0.269
striped bass age 1+ (t-1)
Corbicula clams (t-1)
Centrarchids (t-1)
predatory zooplankton (t-1)
predatory zooplankton
0.358
flow
herbivorous zooplankton (t-1)
herbivorous zooplankton
0.184
temperature
phytoplankton (t-1)
turbidity
c
Suisun
BSMT estuarine fishes (t-1)
BSMT estuarine fishes
0.213
striped bass age 1+ (t-1)
Potamocorbula clams (t-1)
predatory zooplankton (t-1)
predatory zooplankton
0.334
flow
herbivorous zooplankton (t-1)
herbivorous zooplankton
0.331
temperature
phytoplankton (t-1)
turbidity
d
San Joaquin
Mississippi silverside (t-1)
BSMT estuarine fishes (t-1)
BSMT estuarine fishes
0.19
striped bass age 1+ (t-1)
Corbicula clams (t-1)
Centrarchids (t-1)
predatory zooplankton (t-1)
predatory zooplankton
0.336
flow
herbivorous zooplankton (t-1)
herbivorous zooplankton
0.19
temperature
phytoplankton (t-1)
turbidity

**Figure 4.**

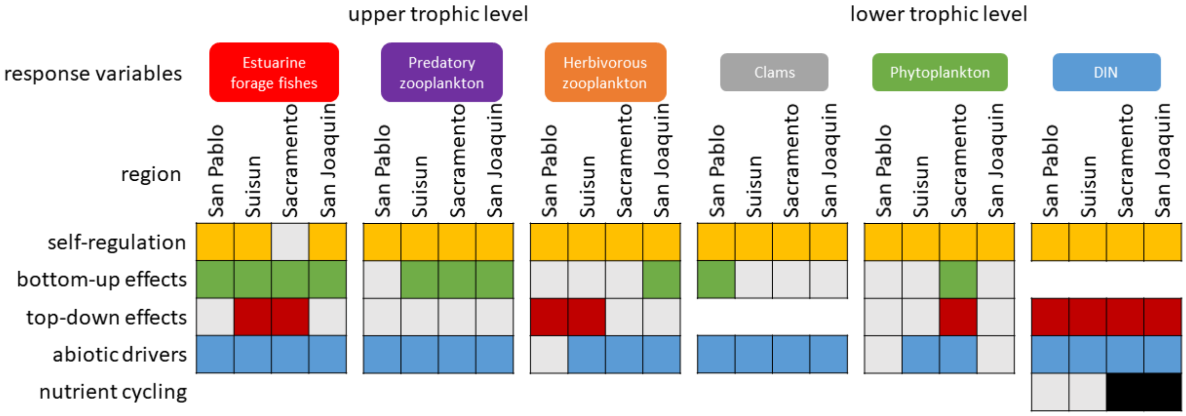
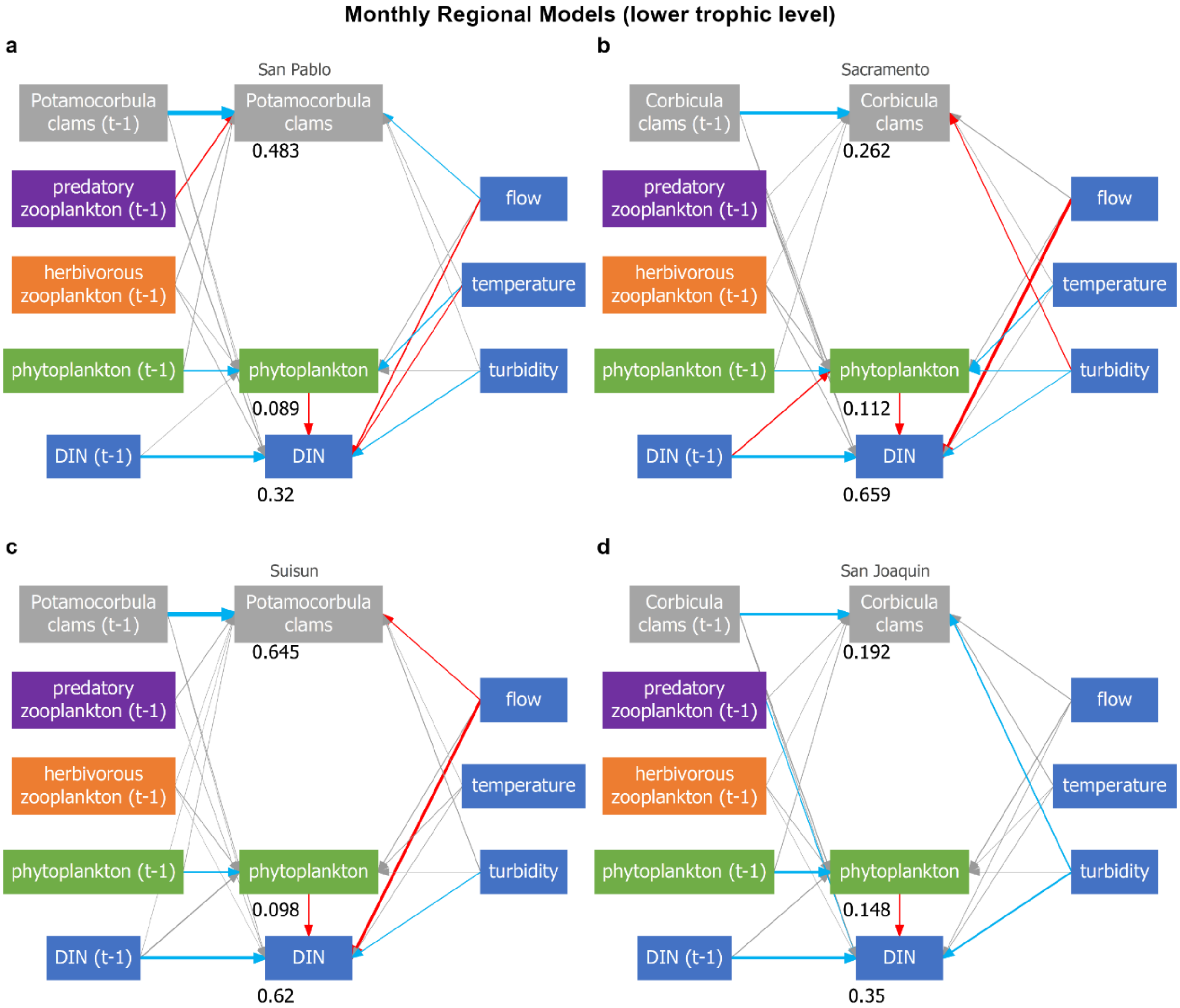

upper trophic level
lower trophic level
response variables
Estuarine forage fishes
Predatory zooplankton
Herbivorous zooplankton
Clams
Phytoplankton
DIN
region
San Pablo
Suisun
Sacramento
San Joaquin
self-regulation
bottom-up effects
top-down effects
abiotic drivers
nutrient cycling

**Figure 5.**



Monthly Regional Models (lower trophic level)
a
San Pablo
Potamocorbula clams (t-1)
predatory zooplankton (t-1)
herbivorous zooplankton (t-1)
phytoplankton (t-1)
DIN (t-1)
Potamocorbula clams
0.483
phytoplankton
0.089
DIN
0.32
flow
temperature
turbidity
b
Sacramento
Corbicula clams (t-1)
predatory zooplankton (t-1)
herbivorous zooplankton (t-1)
phytoplankton (t-1)
DIN (t-1)
Corbicula clams
0.262
phytoplankton
0.112
DIN
0.659
flow
temperature
turbidity
c
Suisun
Potamocorbula clams (t-1)
predatory zooplankton (t-1)
herbivorous zooplankton (t-1)
phytoplankton (t-1)
DIN (t-1)
Potamocorbula clams
0.645
phytoplankton
0.098
DIN
0.62
flow
temperature
turbidity
d
San Joaquin
Corbicula clams (t-1)
predatory zooplankton (t-1)
herbivorous zooplankton (t-1)
phytoplankton (t-1)
DIN (t-1)
Corbicula clams
0.192
phytoplankton
0.148
DIN
0.35
flow
temperature
turbidity

**Figure 6.**

# Evaluating top-down, bottom-up, and environmental drivers of pelagic food web dynamics along an estuarine gradient

**Authors:** Tanya L. Rogers*, Samuel M. Bashevkin*, Christina E. Burdi, Denise D. Colombano, Peter N. Dudley, Brian Mahardja, Lara Mitchell, Sarah Perry, Parsa Saffarinia

*Ecology*

**Appendix S1: Supplemental text, tables, and figures**

## Supplemental methods

### Data processing

Many of the variables were obtained from the Environmental Monitoring Program (EMP), a long-running year-round monitoring program in the SF Estuary with three distinct studies: Zooplankton, Benthic Invertebrates, and Water Quality.

### Invertebrates

Zooplankton abundance data were obtained from the EMP Zooplankton Study (Barros 2021) and Benthic Study (Wells and Interagency Ecological Program 2021), the longest-running and only year-round invertebrate surveys in the SF Estuary. Zooplankton Study data were accessed through the R package ‘zooper’ v2.4.1 (Bashevkin et al. 2022b). Zooplankton were grouped into 6 categories for analysis: cladocerans, herbivorous copepods, predatory copepods, mysids, amphipods, and rotifers (**Table S1**). The herbivorous copepod category included some taxa that are occasionally predatory (e.g., *Limnoithona sinensis*) but only predate on taxa not included in our model (e.g., ciliates). Amphipods were obtained from the Benthic Study because the Zooplankton Study did not record amphipods until 1996 and did not identify them to genus until 2014. Only amphipods routinely found in fish diets (Slater et al. 2019; unpublished data) and in areas sampled by the fish monitoring surveys were included (**Table S1**). Biomass per unit effort (BPUE; µg carbon mass $m^{-3}$ [$m^{-2}$ for amphipods]) was calculated from count data using conversions compiled from the literature by Bashevkin et al. (2022c, 2022b) and Burdi et al. (2021). Since length data were only available for mysids and amphipods, length-mass conversions were used for those taxa while average mass values were used for the other groups. However, since the Benthic Study lacked amphipod length measurements, amphipod BPUE was estimated using the average biomass for each species from the Zooplankton Study (using the genus-level data from 2014 – present), calculated via the length-mass equations.

To check if energy of food resources provided a better model fit than biomass, we additionally calculated energy per unit effort for each zooplankton group (EPUE, J $m^{-3}$ [$m^{-2}$ for amphipods]) using energy density measurements (J $g^{-1}$ dry mass) from the literature. From eight sources (Cummins 1967, Schindler et al. 1971, Vijverberg and Th. Frank 1976, Johnson and Hopkins 1978, Theilacker and Kimball 1984, Yúfera and Pascual 1989, Hanson et al. 1997, Forster 1999), we gathered 36 records of energy density for various types of zooplankton. Of these records, 29 were identified at the species level, two at the genus level, two at the family level, two at the order level, and one at the superorder level. In total, there were 28 unique categories of zooplankton energy density. We matched each of the 28 categories to one of the six categories of zooplankton used in this analysis. This matching gave us two values for amphipods, 12 for cladocerans, 14 for herbivorous copepods, three for predatory copepods, two for mysids, and three for rotifers. We then took averages (**Fig. S8**) to get a value for each category (Dudley et al. 2022). We ultimately did not use EPUE in our analysis as it was highly correlated with BPUE (Pearson $r > 0.99$) and gave very similar results.

The EMP Benthic study was also used to calculate density metrics (count $m^{-2}$) for each of the two invasive clam species (*Potamocorbula amurensis* and *Corbicula fluminea*).

From the Zooplankton Study, annual averages were calculated from 10 stations, while monthly averages were calculated from 15 stations (**Fig. 1, Table S3**). From the Benthic Study, annual averages were calculated from 3 stations while the monthly averages were calculated from 8 stations (**Fig. 1, Table S3**).

### Fish

Fish data were accessed through the R package 'deltafish' v2.2.0 (Bashevkin et al. 2022a, Clark and Bashevkin 2022), which integrates fish monitoring data from the SF Estuary. Most fish monitoring programs in the SF Estuary sample small pelagic fish species or young-of-year fishes in the open water (Tempel et al. 2021). We selected three of the longest-running pelagic fish surveys (Fall Midwater Trawl, FMWT; Summer Townet, STN; San Francisco Bay Study Midwater Trawl, BSMT) and assembled an aggregate biomass index for estuarine forage fishes. The species included in this aggregation were five commonly caught, planktivorous, freshwater-brackish fish species of high management interest: Delta Smelt (*Hypomesus transpacificus*), Longfin Smelt (*Spirinchus thaleichthys*), Threadfin Shad (*Dorosoma petenense*), juvenile American Shad (*Alosa sapidissima*), and age-0 Striped Bass (*Morone saxatilis*) (**Table S1**).

We also assembled data on potential predators and competitors of the estuarine forage fishes. From the BSMT dataset, we produced an aggregate index for planktivorous marine fishes, represented by Northern Anchovy (*Engraulis mordax*) and Pacific Herring (*Clupea pallasii*), which are common in saline waters. We also obtained data for age-1+ Striped Bass from the same dataset as a proxy for piscivorous fishes. From the Delta Juvenile Fish Monitoring Program (DJFMP) beach seine survey, which monitors the littoral fish assemblage, we obtained data for Mississippi Silverside (*Menidia audens*) and fishes from the centrarchid family (**Table S1**). Mississippi Silversides are known to overlap in diet with the pelagic forage fish species and to potentially consume larval fishes (Schreier et al. 2016). Centrarchid fishes are potential predators known to associate with submerged aquatic vegetation, and they have rapidly increased in abundance in the past two decades within the SF Estuary (Brown and Michniuk 2007, Mahardja et al. 2017). Data from the DJFMP beach seine survey were only included in the shorter-term monthly dataset, as year-round sampling only began in 1995, and prior sampling was inconsistent.

To calculate fish BPUE for each species (or species assemblage) in each survey, fork length (mm) of each fish was first converted to biomass in grams using length-weight regression equations from Kimmerer et al. (2005) for the pelagic surveys, and Perry (2020) for the beach seine survey. These biomass measurements were then summed for each sampling occasion (i.e., tow). For the annual dataset, BPUE values were averaged across stations for each region and sampling interval (either month or two-week period), and then averaged again to obtain the annual value. Note that for the BSMT data, only April-October sampling was used to calculate annual values as per Feyrer et al. (2015). For the monthly dataset, only the BSMT and beach seine data were used because the two remaining surveys (STN and FMWT) are seasonal (summer and fall only). BPUE was averaged for each month and station combination, then averaged across stations to obtain monthly BPUE. Alternate stations meant to replace another sampling station in the DJFMP beach seine survey dataset were treated as a single station for the purpose of our analysis (SR012E and SR012W, SJ058E and SJ058W). Beach seine data were only available for the Sacramento and San Joaquin regions, as sampling does not extend to other regions. Annual averages were calculated from 71 stations for the FMWT dataset, 25 stations for the STN dataset, and 10 stations for the BSMT dataset (**Fig. 1, Table S3**). Monthly averages were calculated from 31 stations for the BSMT dataset and nine stations for the DJFMP beach seine survey dataset (**Table S3)**.

### Chlorophyll-a, Nutrients, and Environmental Drivers

Temperature, Secchi depth, chlorophyll-a, and nutrient data were obtained from the EMP Water Quality Study and accessed from an integrated database of discrete water quality monitoring data (Bashevkin et al. 2022d). Data were collected monthly, and stations were selected to ensure consistent coverage over the selected timespan. Chlorophyll-a was used as a proxy for phytoplankton abundance. Nitrogen compounds, specifically ammonia and nitrate, have been proposed as a potential influence in the Delta ecosystem (e.g., Cloern 2001, Richey et al. 2018). However, the nutrients (ammonium, nitrate/nitrite, and phosphorous) were correlated with one another (**Fig. S4**). Due to the complex relationship between different nitrogen forms, we chose to aggregate ammonium and nitrate/nitrite as dissolved inorganic nitrogen (DIN), which represents biologically available nitrogen. We then decided to exclude phosphorous because it is not limiting in the system (Cloern et al. 2020).

Water temperatures were corrected for time-of-day effects by adjusting all measurements to noon using a monthly smooth function of temperature by time-of-day. This smooth function was derived from a generalized additive model fit with the R package mgcv (Wood 2011, Wood et al. 2016) to temperature data from the integrated water quality dataset (Bashevkin et al. 2022d). The model was fit with the code: bam(Temperature ~ Year + te(Longitude, Latitude, day_of_year, d=c(2,1), bs=c('cr', 'cc'), k=c(25, 13), by=Year) + te(Time, day_of_year, bs=c('cr', 'cc'), k=c(5, 13)), data = Data, method='fREML', discrete=T). As a measure of turbidity, we used negative secchi depth, so that higher values would mean higher turbidities and aid in interpretation. Salinity was considered but excluded as a driver because it was highly correlated with flow (**Fig. S4**). Flow is also more directly controlled by management.

For nutrient data values below reporting limits (RL), we substituted the values below the RL with simulated values drawn from a uniform distribution U(0.001, RL) (Helsel 2011). One simulation was run for each parameter and a seed was set prior to running the simulation to ensure reproducibility. When historic reporting limits were not always reported, we used the most common historical RL (0.01) for the nutrient parameters.

Prior to computing regional and temporal averages, we imputed missing values for each variable at each station by fitting autoregressive integrated moving average (ARIMA) models. ARIMA models are time series models that account for dependence on prior values and longer-term values. We specified ARIMA models that explicitly account for seasonality and allow drift (non-stationarity), and then identified the best fit model using Akaike Information Criterion (AIC). Using the best fit model, we applied a Kalman filter to impute missing values in the time series. Then we evaluated performance by checking the residuals, autocorrelation, and accuracy. These functions were performed using the R package 'forecast' (Hyndman and Khandakar 2008, Hyndman et al. 2022).

We obtained flow data from the Dayflow dataset made available by the California Department of Water Resources (DWR) (https://data.cnra.ca.gov/dataset/dayflow). This dataset provides modeled daily flows, calibrated by several USGS gaging stations, for upstream reaches which flow into the SF Estuary as well as estimates of net inflows and outflows. For the annual dataset, total outflow (QTOT) was used. For the regional datasets, outflow at Rio Vista (QRIO) was used for the Sacramento region, San Joaquin River flow past Jersey point (QWEST) for the San Joaquin region, and total outflow for both the Suisun and San Pablo regions. For the annual datasets, daily flows were averaged by water year (1 October – 30 September), while for the monthly dataset, daily flows were averaged by month.

## Analysis

Converting the conceptual model into SEMs required simplification to facilitate implementation and interpretation. For instance, were we to fit the complete conceptual model to the annual dataset, the number of free parameters would vastly exceed the number of data points. Thus, each SEM model employed only a subset of variables and (in many cases) species aggregates rather than finer taxonomic groups.

The annual models employed a latent variable for estuarine fishes. Since latent variables require that the manifest variables be correlated in order to extract a common trend, the BSMT dataset was dropped from the Sacramento region because it was not correlated with the other two fish surveys (FMWT and STN; **Fig. S3**). Only the BSMT dataset was used in the monthly models because it was the only survey with year-round monthly sampling.

To compute the total effect size of each interaction type in the monthly models, the lagged effect of a species on itself was considered ‘self-regulation,’ the effect of all lower trophic levels (including nutrients on phytoplankton) was considered ‘bottom-up,’ the effect of all higher trophic levels was considered ‘top-down,’ the effect of all abiotic drivers (flow, temperature, turbidity) was considered ‘environmental,’ and the effect of all consumers (zooplankton, clams) on nutrients was considered ‘nutrient cycling.’ The structure of the monthly SEMs was very similar to a vector autoregressive model, but where food web structure places constraints on the predictor variables used.

If a time series contained zeros, the minimum nonzero value was added to all values prior to log transformation. For flow values in the regional datasets, which were sometimes negative, the largest negative value was subtracted prior to this procedure. Removal of seasonality from the monthly data was done after log transformation, but before scaling. For both regional datasets (annual and monthly), all data transformations were done within each region.

We assessed model fit using a chi-squared test, which tests the hypothesis that the predicted and observed covariance matrices are equal. If this test was statistically significant ($p<0.05$), indicating lack of model fit, we examined the residual covariance among variables, and modified the original model (added additional paths or covariances) to better account for these residual relationships. We only added paths that improved model fit, and that were biologically reasonable and consistent with our knowledge of the natural history of the system.

## Supplemental Discussion (SF Estuary-specific findings)

Top-down effects of predatory zooplankton on herbivorous zooplankton were not observed in the model of upper trophic level aggregates, and among individual zooplankton groups, negative top-down effects were only detected in Sacramento (between predatory and herbivorous copepods). Thus, we did not find strong support for top-down trophic control among plankton functional groups, although variation in zooplankton community composition and complex interactions within and among functional groups may limit our ability to resolve this. For instance, several of the species we considered herbivorous (since they do not predate on other taxa in our model) are actually omnivorous (e.g. *Limnoithona* spp*.*, *P. forbesi*) and predate on smaller microzooplankton (e.g. ciliates) (Bouley and Kimmerer 2006, York et al. 2014) which are not monitored well in the SF Estuary.

We detected top-down effects of fishes on herbivorous (but not predatory) zooplankton, consistent with findings that fishes in the SF Estuary (e.g., Striped Bass, Delta Smelt, Longfin Smelt) positively select for herbivorous copepods over other available zooplankton prey (Bryant and Arnold 2007, Slater and Baxter 2014, Barros et al. 2022, Lojkovic Burris et al. 2022). This could be partially due to predatory copepods having a lower nutritional value than herbivorous copepods (Kratina and Winder 2015). At the top of the food web, we did not detect any negative effects of other fish groups on estuarine fishes, although this may reflect deficiencies in the monitoring data (see main text). We did detect a positive effect of age 1+ striped bass on estuarine fishes in Suisun, but this could be partially explained by self-regulation since younger striped bass were included in the estuarine fishes metric.

The positive relationships of *Corbicula* with zooplankton in the individual zooplankton and annual models were unexpected. One possible explanation for this pattern in the annual model is that the direction of causality may be reversed. The annual models did not incorporate time-lags, so we were unable to use them to investigate specific directions of the causality in each relationship as we did in the monthly models. It is possible that annual zooplankton abundance is positively related to *Corbicula* abundance since zooplankton are a food source for *Corbicula*. A second possible explanation is that the count data we obtained for *Corbicula* may not be fully representative of their feeding impact since clearance rates are strongly related to clam size (Lauritsen 1986), which was not represented in our data. Lastly, *Corbicula* tend to be found in higher abundance in constructed canals (Eng 1979) and shallow water (Benson and Williams 2021) whereas our data were mostly collected in deeper channels. Thus, the counts we used may not be entirely reflective of their true population size and top-down impact on zooplankton.

Our study is the first to find strong evidence for a bottom-up relationship between chlorophyll and zooplankton biomass in the current regime. However, past studies have found this link before the clam and zooplankton invasions induced a regime shift (Orsi and Mecum

1986), or have weakly linked chlorophyll to zooplankton growth rates (Kimmerer et al. 2018, Gearty et al. 2021, yet see Kimmerer et al. 2014). Furthermore, Mac Nally et al. (2010) found weak evidence for spring chlorophyll as a driver of spring calanoid and summer mysid biomass.

Flow had predominantly positive effects on herbivorous zooplankton but negative effects on predatory zooplankton. This could be due to salinity-driven biotic interactions, as certain predatory zooplankton (e.g., *Acartiella sinensis*), along with *Potamocorbula,* limit the distribution of herbivorous zooplankton via predation (Slaughter et al. 2016, Kayfetz and Kimmerer 2017); however, most predatory species occur in more saline waters and shift downstream with high flows.

Turbidity had largely positive effects on DIN, zooplankton, and fish, except in Suisun where effects on zooplankton were more negative. The SF Estuary was historically turbid, and turbidity is a key habitat requirement for native species such as Delta Smelt (Thomson et al. 2010, Feyrer et al. 2011) so species are expected to benefit from more turbid conditions. Furthermore, turbidity could be associated with abundance of detrital plant material that can serve as an important, selected-for food source for zooplankton (Harfmann et al. 2019, Jeffres et al. 2020).

## Supplemental Tables

**Table S1.** List of taxonomic groups used in our analysis, their dominant feeding strategies, and their constituent taxa.

| Category | Feeding Strategy | Taxon name |
|---|---|---|
| Cladocerans | Herbivorous | *Bosmina longirostris*<br>*Daphnia* spp.<br>*Diaphanosoma* spp.<br>Other Cladocera |
| Herbivorous Copepods | Herbivorous | *Acartia* spp.<br>Diaptomidae<br>*Eurytemora affinis*<br>*Pseudodiaptomus* spp. |

| | | |
|---|---|---|
| | | *Pseudodiaptomus forbesi*<br>*Pseudodiaptomus marinus*<br>*Sinocalanus doerrii*<br>Cirripedia larvae<br>Copepod larvae<br>Harpacticoida |
| | Omnivorous | *Limnoithona* spp.<br>*Limnoithona sinensis*<br>*Limnoithona tetraspina* |
| Mysids | Predatory | *Hyperacanthomysis longirostris*<br>*Neomysis mercedis*<br>*Orientomysis aspera*<br>*Alienacanthomysis macropsis*<br>*Deltamysis holmquistae*<br>*Neomysis kadiakensis* |
| Predatory Copepods | Predatory | *Acartiella sinensis*<br>*Tortanus* spp.<br>*Acanthocyclops* spp.<br>*Oithona* spp.<br>*Oithona davisae*<br>*Oithona similis* |
| Rotifers | Predatory | *Asplanchna* spp. |
| | Herbivorous | *Keratella* spp.<br>*Polyarthra* spp.<br>*Synchaeta* spp.<br>*Trichocerca* spp. |
| Amphipods | Herbivorous | *Ampelisca* spp.<br>*Monocorophium* spp.<br>*Sinocorophium* spp.<br>*Gammarus* spp.<br>*Americorophium* spp.<br>*Crangonyx* spp.<br>*Hyalella* spp. |
| Estuarine fishes | Planktivorous | Delta Smelt (*Hypomesus transpacificus*)<br>Longfin Smelt (*Spirinchus thaleichthys*)<br>Threadfin Shad (*Dorosoma petenense*)<br>American Shad, juvenile (*Alosa sapidissima*)<br>Striped Bass, age 0 (*Morone saxatilis*) |
| Marine fishes | Planktivorous | Northern Anchovy (*Engraulis mordax*)<br>Pacific Herring (*Clupea pallasii*) |
| Mississippi Silverside | Planktivorous | *Menidia audens* |
| Striped Bass | Piscivorous | *Morone saxatilis* (age 1+) |
| Centrarchid fishes | Piscivorous | Largemouth Bass (*Micropterus salmoides*)<br>Smallmouth Bass (*Micropterus dolomieu*)<br>Bluegill (*Lepomis macrochirus*)<br>Redear sunfish (*Lepomis microlophus*) |

**Table S2.** Variable definitions and temporal extent for the monthly and annual datasets.

| Variable | Monthly years (missing months) | Annual years (missing years) | Definition |
|---|---|---|---|
| Ammonia | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Amphipods catch | 1997–2020 (18) | 1975–2020 (1) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Amphipods mass | 1997–2020 (18) | 1975–2020 (1) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Centrarchids DJFMP | 1995–2020 (3) | | year-round - beach seines - biomass |
| Cladocera | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Cladocera catch | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Cladocera energy | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Corbicula | 1997–2020 (18) | 1975–2020 (1) | from the Environmental Monitoring Program (EMP) Benthic Survey at DWR - year-round |
| Delta smelt BSMT | 1995–2020 (38) | 1980–2020 (1) | year-round - midwater trawl - biomass |
| Delta smelt BSOT | 1995–2020 (18) | 1980–2020 (0) | year-round - otter trawl - biomass |
| Delta smelt FMWT | | 1975–2020 (1) | fall (September - December) - midwater trawl - biomass |

|  |  |  |  |
|---|---|---|---|
| Delta smelt STN |  | 1975–2021 (0) | summer (June - August) - townet - biomass |
| Dissolved Inorganic Nitrogen | 1995–2020 (0) |  | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Dissolved Orthophos | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Estuarine fishes BSMT | 1995–2020 (38) | 1980–2020 (1) | year-round - midwater trawl - biomass of estuarine pelagic forage fishes |
| Estuarine fishes BSOT | 1995–2020 (18) | 1980–2020 (0) | year-round - otter trawl - biomass of estuarine pelagic forage fishes |
| Estuarine fishes FMWT |  | 1975–2020 (1) | fall (September - December) - midwater trawl - biomass of estuarine pelagic forage fishes |
| Estuarine fishes STN |  | 1975–2021 (0) | summer (June - August) - townet - biomass of estuarine pelagic forage fishes |
| Flow | 1995–2020 (0) | 1975–2020 (0) | year-round - mean Delta outflow (water leaving the Delta to the Bay) |
| Herbivorous copepods | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Herbivorous copepods catch | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Herbivorous copepods energy | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Herbivorous zooplankton biomass | 1995–2020 (2) | 1975–2020 (0) | summed herbivorous zooplankton biomass |

| | | | |
|---|---|---|---|
| Herbivorous zooplankton energy | 1995–2020 (2) | 1975–2020 (0) | summed herbivorous zooplankton energy |
| Longfin smelt BSMT | 1995–2020 (38) | 1980–2020 (1) | year-round - midwater trawl - biomass |
| Longfin smelt BSOT | 1995–2020 (18) | 1980–2020 (0) | year-round - otter trawl - biomass |
| Longfin smelt FMWT | | 1975–2020 (1) | fall (September - December) - midwater trawl - biomass |
| Longfin smelt STN | | 1975–2021 (0) | summer (June - August) - townet - biomass |
| Marine fishes BSMT | 1995–2020 (38) | 1980–2020 (1) | year-round - midwater trawl - biomass |
| Marine fishes BSOT | 1995–2020 (18) | 1980–2020 (0) | year-round - otter trawl - biomass |
| Marine fishes FMWT | | 1975–2020 (1) | fall (September - December) - midwater trawl - biomass |
| Marine fishes STN | | 1975–2021 (0) | summer (June - August) - townet - biomass |
| Mississippi silverside DJFMP | 1995–2020 (3) | 1976–2020 (0) | year-round - beach seines - biomass |
| Mysids | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Mysids catch | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |

| | | | |
|---|---|---|---|
| Mysids energy | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Nitrate and Nitrite | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Phytoplankton | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Potamocorbula | 1997–2020 (18) | 1975–2020 (1) | from the Environmental Monitoring Program (EMP) Benthic Survey at DWR - year-round |
| Predatory copepods | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Predatory copepods catch | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Predatory copepods energy | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Predatory zooplankton biomass | 1995–2020 (2) | 1975–2020 (0) | summed predatory zooplankton biomass |
| Predatory zooplankton energy | 1995–2020 (2) | 1975–2020 (0) | summed predatory zooplankton energy |
| Rotifers catch | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Rotifers energy | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |
| Rotifers mass | 1995–2020 (2) | 1975–2020 (0) | from 5 different sources - year-round - see Bashevkin et al. 2022 |

|  |  |  |  |
|---|---|---|---|
| Secchi | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Striped bass age 1+ BSMT | 1995–2020 (38) |  | year-round - midwater trawl - biomass of age 1+ individuals |
| Striped bass age 1+ BSOT | 1995–2020 (18) |  | year-round - otter trawl - biomass of age 1+ individuals |
| Striped bass BSMT | 1995–2020 (38) | 1980–2020 (1) | year-round - midwater trawl - biomass of age 0 individuals |
| Striped bass BSOT | 1995–2020 (18) | 1980–2020 (0) | year-round - otter trawl - biomass of age 0 individuals |
| Striped bass FMWT |  | 1975–2020 (1) | fall (September - December) - midwater trawl - biomass of age 0 individuals |
| Striped bass STN |  | 1975–2021 (0) | summer (June - August) - townet - biomass of age 0 individuals |
| Temperature | 1995–2020 (0) | 1980–2020 (0) | from the Discrete Environmental Monitoring Program (EMP) at DWR - year-round |
| Total zooplankton biomass | 1995–2020 (2) | 1975–2020 (0) | summed zooplankton biomass |
| Total zooplankton energy | 1995–2020 (2) | 1975–2020 (0) | summed zooplankton energy |
| Turbidity | 1995–2020 (0) | 1980–2020 (0) | negative secchi depth |

**Table S3.** Stations used to calculate input data for annual and monthly models.

| Survey | Temporal resolution | Stations |
|---|---|---|

| | | |
|---|---|---|
| Bay Study | Annual | 427, 428, 429, 431, 432, 433, 534, 535, 736, 837 |
| DJFMP | Annual | MS001N, SJ001S, SJ005N, SR012E, SR012E, SR014W, TM001N |
| EMP Benthic | Annual | D4-L, D7-C, D28A-L |
| EMP Nutrients | Annual | D26, D28A, D4, D6, D7, D8 |
| EMP Zoop | Annual | NZD28, NZ054, NZ074, NZ048, NZ086, NZ064, NZ060, NZ028, NZS42, NZ032 |
| FMWT | Annual | 338, 339, 401, 403, 404, 405, 406, 407, 408, 409, 410, 411, 412, 413, 414, 415, 416, 417, 418, 501, 502, 503, 504, 505, 507, 508, 509, 510, 511, 512, 513, 515, 516, 517, 518, 519, 601, 602, 603, 604, 605, 606, 608, 701, 703, 704, 705, 706, 707, 708, 709, 710, 711, 802, 804, 806, 807, 808, 809, 810, 811, 812, 813, 814, 815, 902, 904, 905, 906, 908, 915 |
| STN | Annual | 405, 411, 418, 501, 504, 508, 513, 519, 520, 602, 606, 609, 610, 704, 706, 707, 711, 801, 804, 809, 812, 815, 902, 906, 915 |
| Bay Study | Monthly | 317, 318, 319, 320, 321, 322, 323, 325, 427, 428, 429, 430, 431, 432, 433, 534, 535, 736, 837, 345, 346, 447, 750, 751, 752, 853, 760, 761, 863, 864, 865 |
| DJFMP | Monthly | SR014W, SR012E, MS001N, TM001N, SJ005N, SJ001S, OR003W, OR014W, SR012E |
| EMP Benthic | Monthly | D4-L, D6-R, D7-C, D16-L, D28A-L, D24-L, D41-C, D41A-C |
| EMP Nutrients | Monthly | D26, D28A, D4, D41, D6, D7, D8 |
| EMP Zoop | Monthly | NZD28, NZ054, NZ074, NZ048, NZD16, NZ086, NZ064, NZ060, NZ028, NZS42, NZ032, NZD41, NZD06 |

**Table S4.** Empirical support and justification for paths in conceptual model.

| Arrow start | Arrow end | Explanation |
|---|---|---|

| | | |
|---|---|---|
| Estuarine forage fishes | Predatory fishes | The introduced Striped Bass and Largemouth Bass are potentially important predators of the estuarine forage fish species. Striped Bass may have exerted top-down control on smaller-sized fishes for decades (Nobriga and Smith 2020) and consumption by sub-adults partly sampled by the surveys in this study may be quite significant (Loboschefsky et al. 2012). Largemouth Bass is a highly prolific piscivore in the freshwater portion of the SF Estuary and associated with the rapidly expanding invasive submersed aquatic vegetation (Conrad et al. 2016, Mahardja et al. 2017). |
| Estuarine forage fishes | Competing fishes | When zooplankton levels declined after the clam *Potamocorbula* was introduced in the 1980s, distribution of the planktivorous and marine-oriented Northern Anchovy (*Engraulis mordax*) shifted towards higher salinity in the SF Estuary, indicating some overlap in diet with estuarine forage fishes (Kimmerer 2006). The highly abundant and widely distributed Mississippi Silverside (*Menidia audens*) has been considered as both competitor and intraguild predator of the endangered Delta Smelt, a species included in the estuarine forage fish group (Baerwald et al. 2012, Mahardja et al. 2016). |
| Zooplankton | Estuarine forage fishes | The estuarine forage fishes in these models eat zooplankton at all life stages included within this category (Feyrer et al. 2003, Kimmerer 2006, Slater et al. 2019). |
| Pred. copepods | Pred. copepods | Predatory copepods feed on other predator copepods in this dataset (Kerfoot 1978, Li and Li 1979) |
| Pred. copepods | Mysids | Mysids (including native species) feed on copepods (Wilson 1951, Knutson and Orsi 1983) |
| Herb. copepods | Pred. copepods | Predatory copepods consume herbivorous copepods: (Kayfetz and Kimmerer 2017) |
| Herb. copepods | Mysids | Mysids (including native species) feed on copepods (Wilson 1951, Knutson and Orsi 1983) |
| Cladocerans | Pred. copepods | Predatory copepods such as *Acanthocyclops* feed on cladocerans (Gliwicz and Stibor 1993) |
| Pred. copepods | Clams | *Potamocorbula* consumes copepod nauplii (Kimmerer et al. 1994). |

| | | |
|---|---|---|
| Herb. copepods | Clams | *Potamocorbula* consumes copepod nauplii (Kimmerer et al. 1994). |
| Phytoplankton | Clams | The invasive clams consume phytoplankton (Alpine and Cloern 1992**).** |
| Phytoplankton | Herb. copepods | Herbivorous copepods consume phytoplankton (Orsi 1995) |
| Phytoplankton | Cladocerans | Cladocerans consume phytoplankton (Orsi 1995). |
| Phytoplankton | Amphipods | Amphipods consume phytoplankton such as diatoms (Durand 2015) |
| Phytoplankton | Rotifers | Rotifers consume phytoplankton (Walz 1995) |
| Nitrate/Nitrite | Phytoplankton | Phytoplankton have some control over nitrate concentrations (Peterson et al. 1985). |
| Ammonia | Phytoplankton | Phytoplankton have some control over ammonia concentrations (Peterson et al. 1985). |
| Phosphorous | Phytoplankton | Phytoplankton have some control over phosphorous concentrations (Peterson et al. 1985). |
| All biotic variables | Flow | Flow is a strong driver of species abundance and distribution in the SF Estuary (Kimmerer 2002) |
| All biotic variables | Temperature | Temperature impacts food webs from sub-cellular to community scales (Petchey et al. 1999, Clarke 2006, Herbold et al. 2022) |
| All biotic variables | Turbidity | Turbidity is an important indicator of habitat in the SF Estuary (Feyrer et al. 2007) |

**Table S5.** Overview of endogenous (response) and exogenous variable for each SEM.

| Spatiotemporal resolution (submodel) | Endogenous variables | Exogenous variables |
|---|---|---|
| Annual | Phytoplankton<br>Herbivorous zooplankton<br>Predatory zooplankton<br>Estuarine fishes | Clams<br>Flow<br>Temperature<br>Turbidity |
| Annual-regional | Phytoplankton<br>Herbivorous zooplankton<br>Predatory zooplankton<br>Estuarine fishes | Clams<br>Flow<br>Temperature<br>Turbidity |
| Monthly-regional (upper trophic level) | Herbivorous zooplankton<br>Predatory zooplankton<br>Estuarine fishes | Clams<br>Phytoplankton<br>Age 1+ Striped Bass<br>Mississippi Silversides<br>Centrarchid fishes<br>Flow<br>Temperature<br>Turbidity<br>Lagged endogenous variables |

| | | |
|---|---|---|
| Monthly-regional (lower trophic level) | Phytoplankton<br>Clams<br>DIN | Herbivorous zooplankton<br>Predatory zooplankton<br>Flow<br>Temperature<br>Turbidity<br>Lagged endogenous variables |
| Monthly-regional (zooplankton groups) | Phytoplankton<br>Rotifers<br>Amphipods<br>Cladocerans<br>Herbivorous copepods<br>Predatory copepods<br>Mysids | Clams<br>Flow<br>Temperature<br>Turbidity<br>Lagged endogenous variables |

## Supplemental Figures

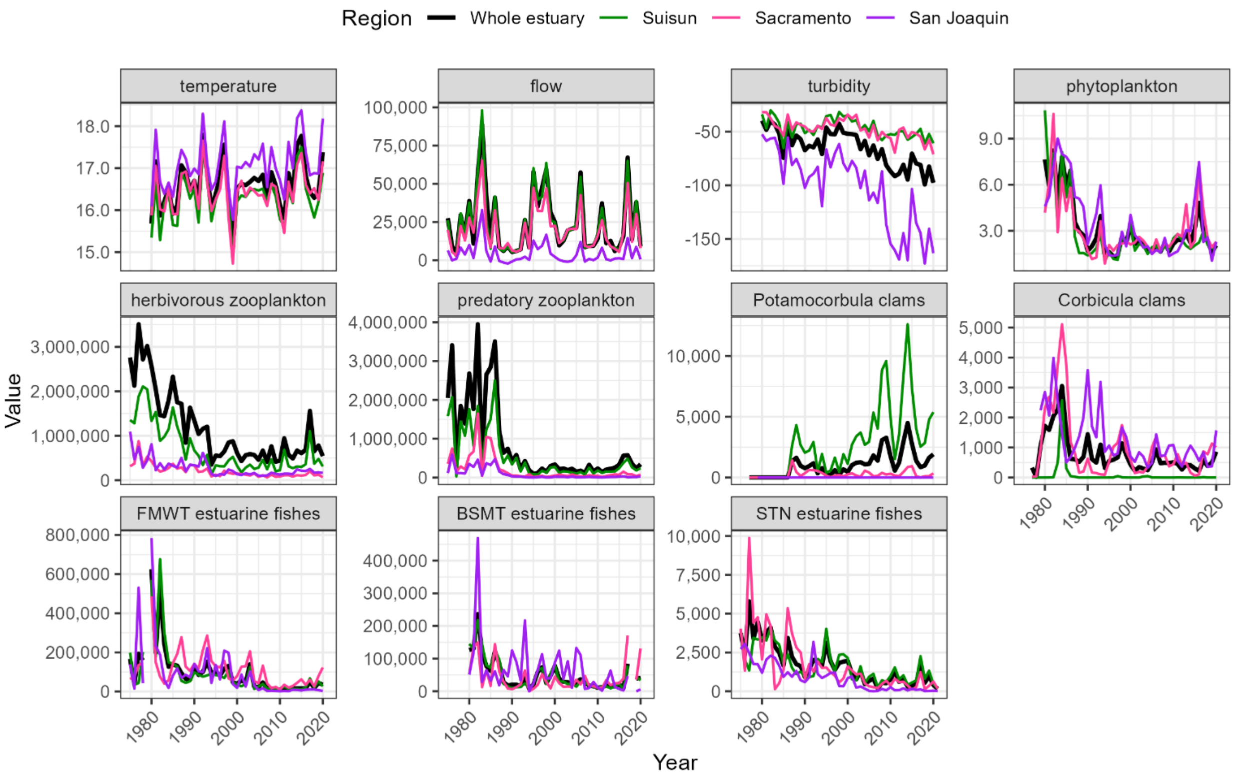


**Figure S1.** Annual time series. FMWT = Fall Midwater Trawl, BSMT = Bay Study Midwater Trawl, STN = Summer Townet.

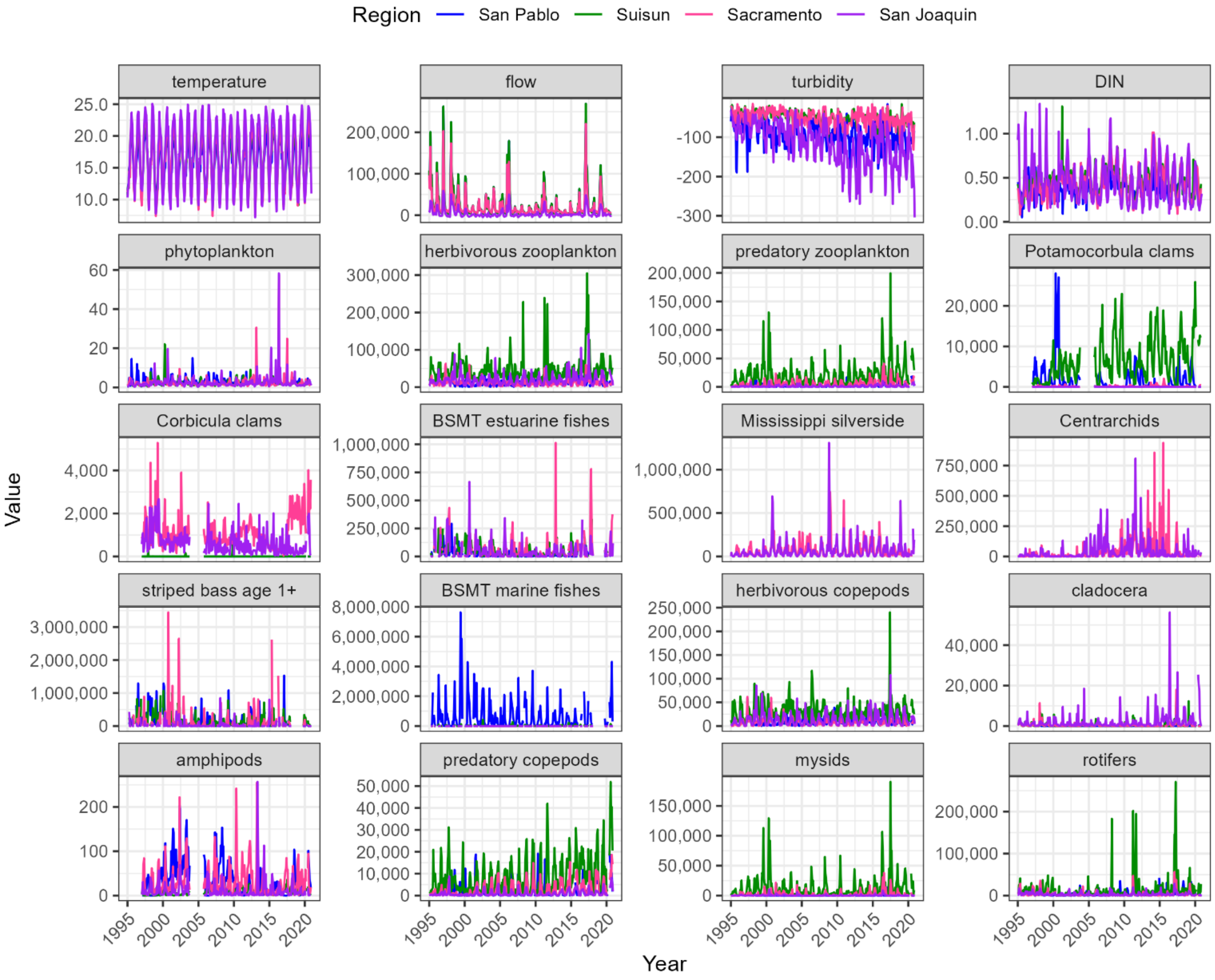


**Figure S2.** Monthly time series. DIN = dissolved inorganic nitrogen, BSMT = Bay Study Midwater Trawl.

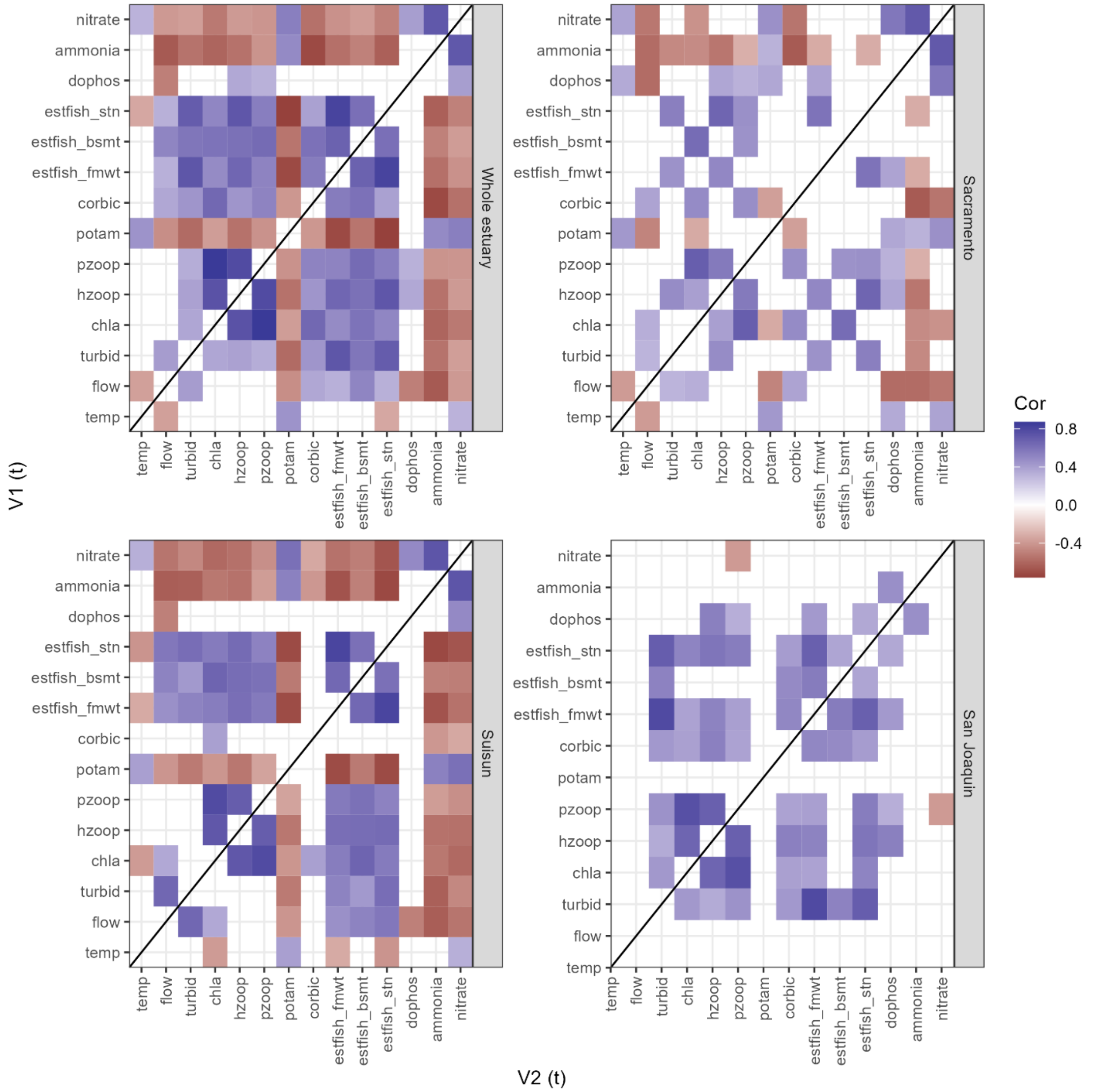


**Figure S3.** Cross-correlation matrices for the annual dataset with no lag. V1 and V2 refer to the different variables for which the correlation is calculated, while t refers to the timepoint at which their correlation is calculated. Abbreviated variable names are as follows: dophos = dissolved orthophosphate, estfish_stn = estuarine fishes from the Summer Townet survey, estfish_bsmt = estuarine fishes from the Bay Study Midwater Trawl, estfish_fmwt = estuarine fishes from the Fall Midwater Trawl, corbic = *Corbicula*, potam = *Potamocorbula*, pzoop = predatory zooplankton, hzoop = herbivorous zooplankton, chla = chlorophyll a, turbid = turbidity, temp = temperature.

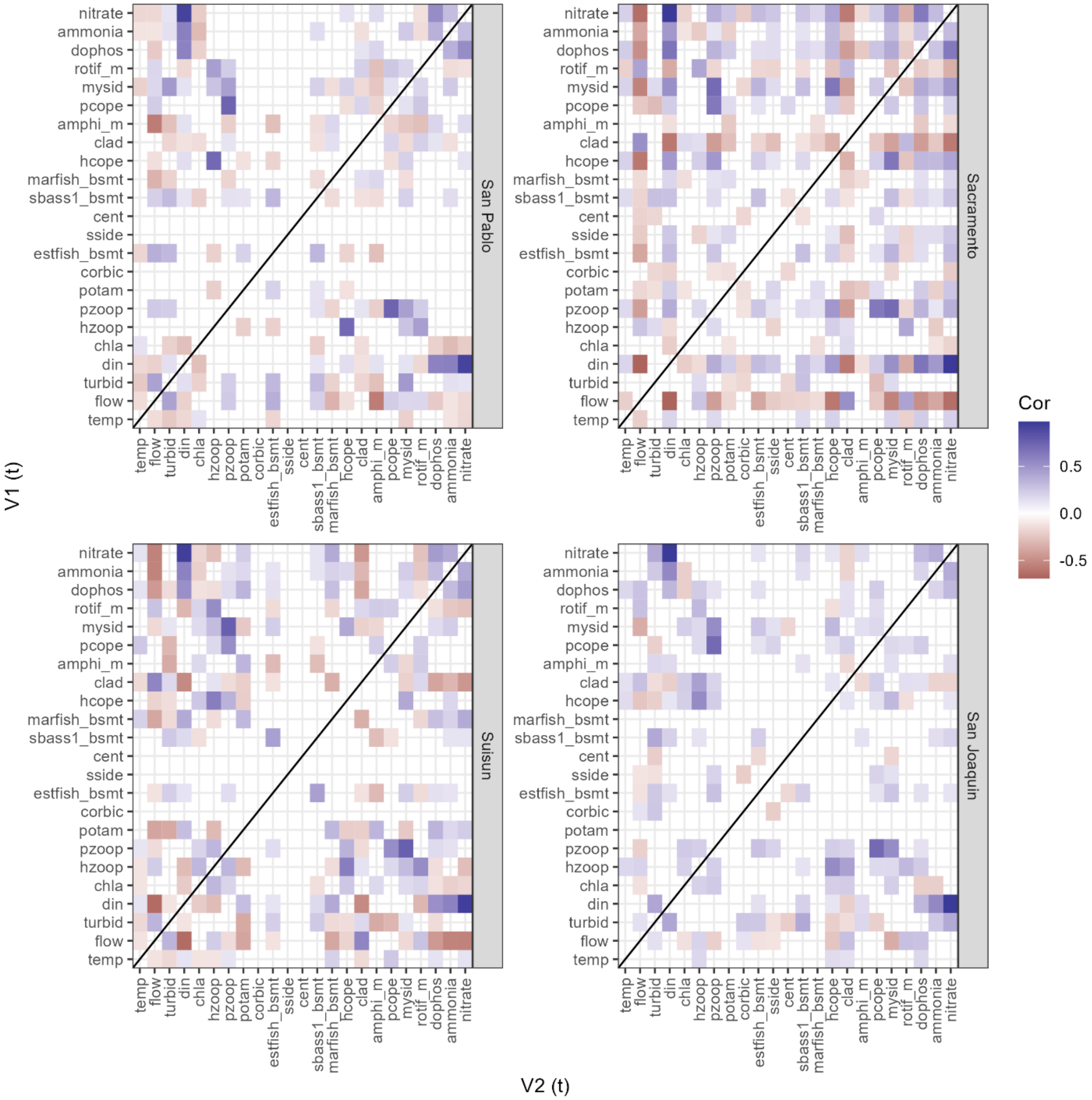


**Figure S4.** Cross-correlation matrices for the monthly dataset with no lag. Abbreviated variable names are as follows: dophos = dissolved orthophosphate, rotif_m = rotifers, pcope = predatory copepods, amphi_m = amphipods, clad = cladocerans, hcope = herbivorous copepods, marfish_bsmt = marine fishes from the Bay Study Midwater Trawl, sbass1_bsmt = Striped Bass age 1+ from the Bay Study Midwater Trawl, cent = Centrarchids, sside = Mississippi Silversides, estfish_bsmt = estuarine fishes from the Bay Study Midwater Trawl, corbic = *Corbicula*, potam = *Potamocorbula*, pzoop = predatory zooplankton, hzoop = herbivorous zooplankton, chla = chlorophyll a, din = dissolved inorganic nitrogen, turbid = turbidity, temp = temperature.

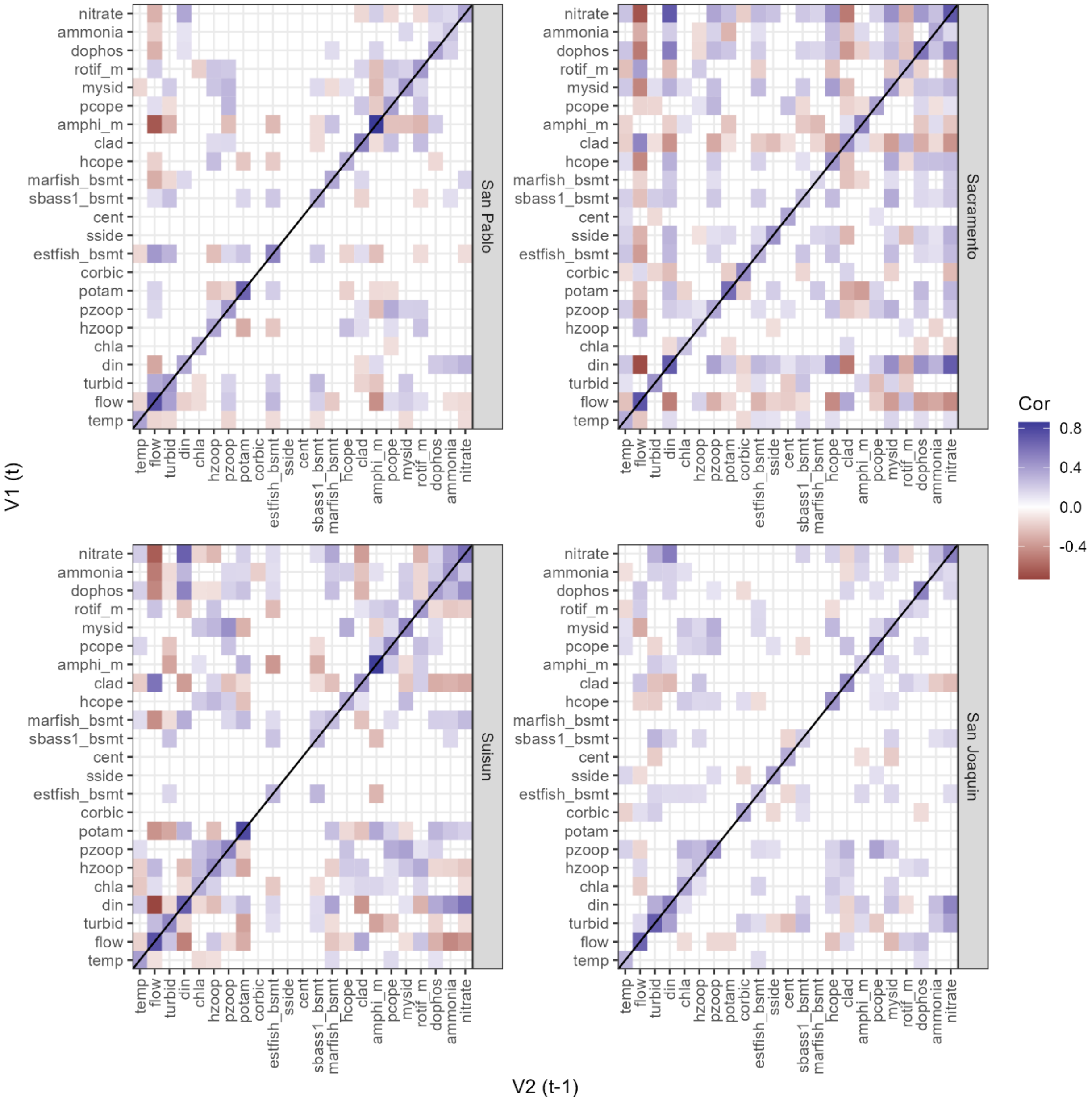


**Figure S5.** Cross-correlation matrices for the monthly dataset with a lag of 1 month. See **Fig. S4** for abbreviated variable name definitions.

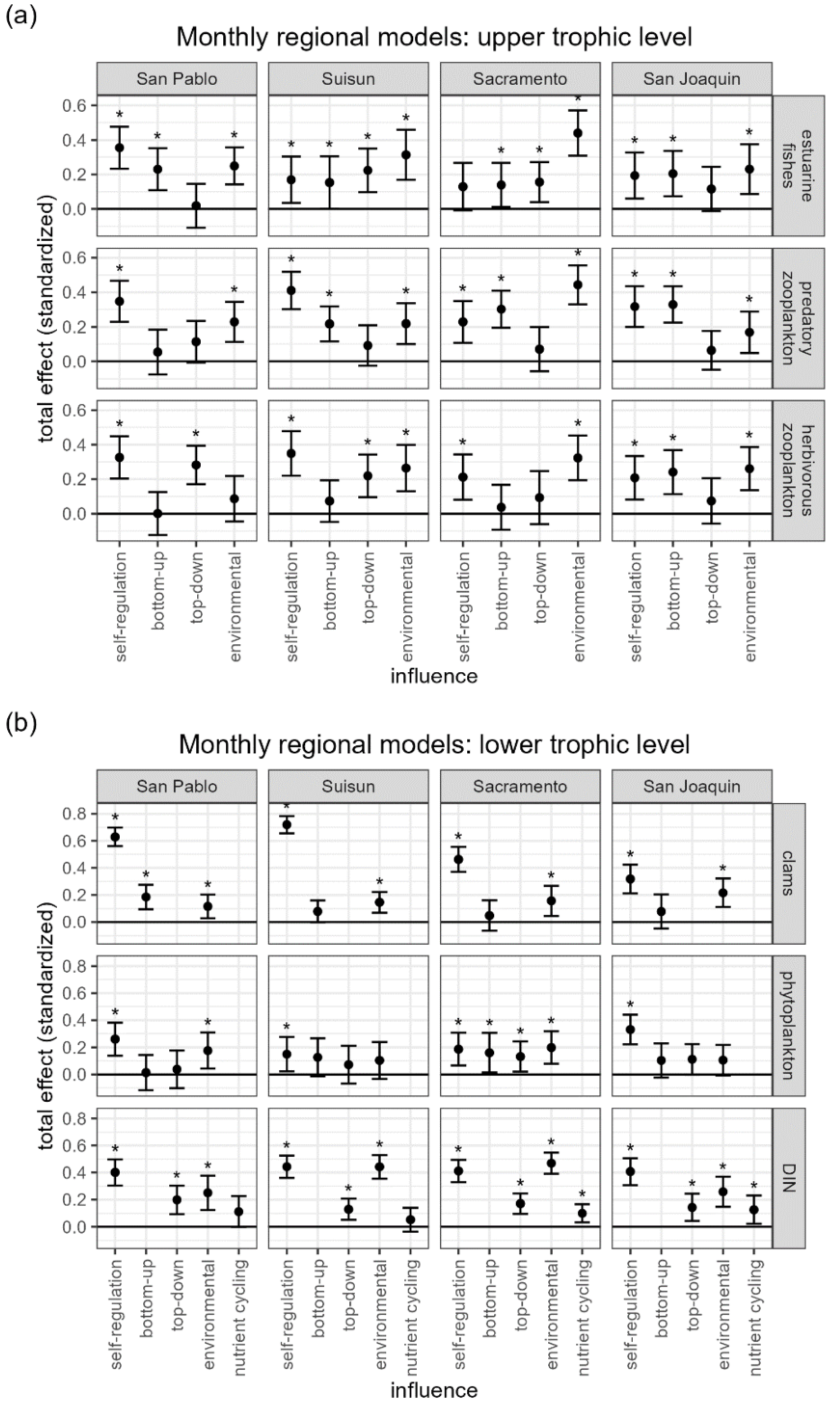


**Figure S6**. Total effect sizes for different interaction types in monthly-regional SEMs using (a) upper and (b) lower trophic level aggregates. * = total effect significant (p<0.05)

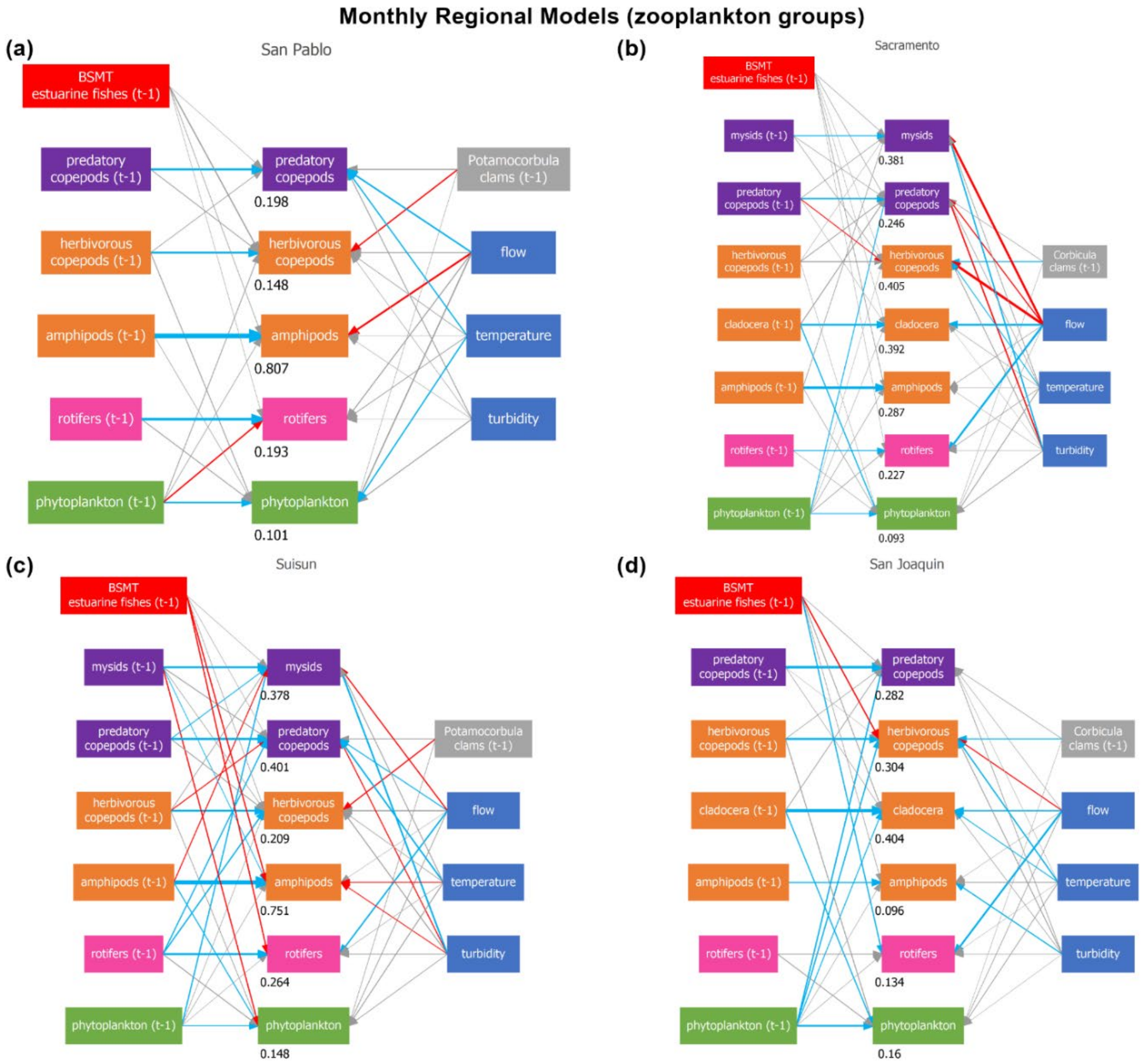


**Figure S7**. Path diagrams for monthly-regional SEMs using individual zooplankton groups. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate coefficients not significantly different from 0. Arrow thickness is proportional to the magnitude of the standardized path coefficient. Numbers next to each variable are associated $R^2$ values. Colors of variables match the colors in the conceptual model.

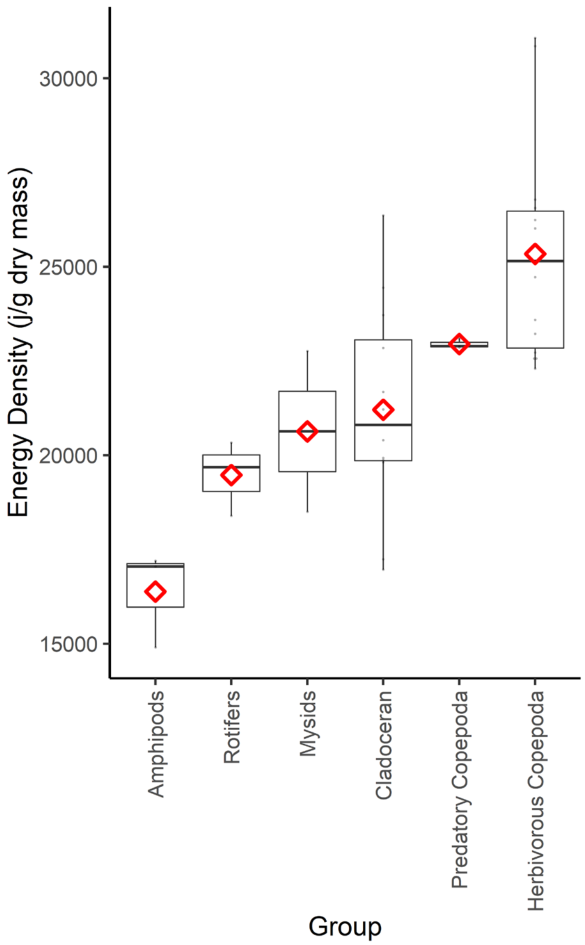


**Figure S8.** Box plot of the energy densities for the six categories of zooplankton used in this analysis. Red diamonds represent the mean values.

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