








## ARTICLE

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

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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 (SEMs) 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

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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 data sets can be leveraged to generate insights across multiple scales.

#### KEYWORDS

bottom-up, estuaries, fish, food webs, invasive species, long-term monitoring, phytoplankton, structural equation model, top-down, zooplankton

## 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 & 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 & 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 & Nagelkerken, 2020). Studies along estuarine gradients have examined how top-down, bottom-up, and environmental drivers affect benthic species (e.g., Hauxwell et al., 1998; Kimbro et al., 2019; Leonard et al., 1998) 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 nonestuarine 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 & 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 & 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 (Feyrer et al., 2015; Mac Nally et al., 2010). 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 posed 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? (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 toward southern

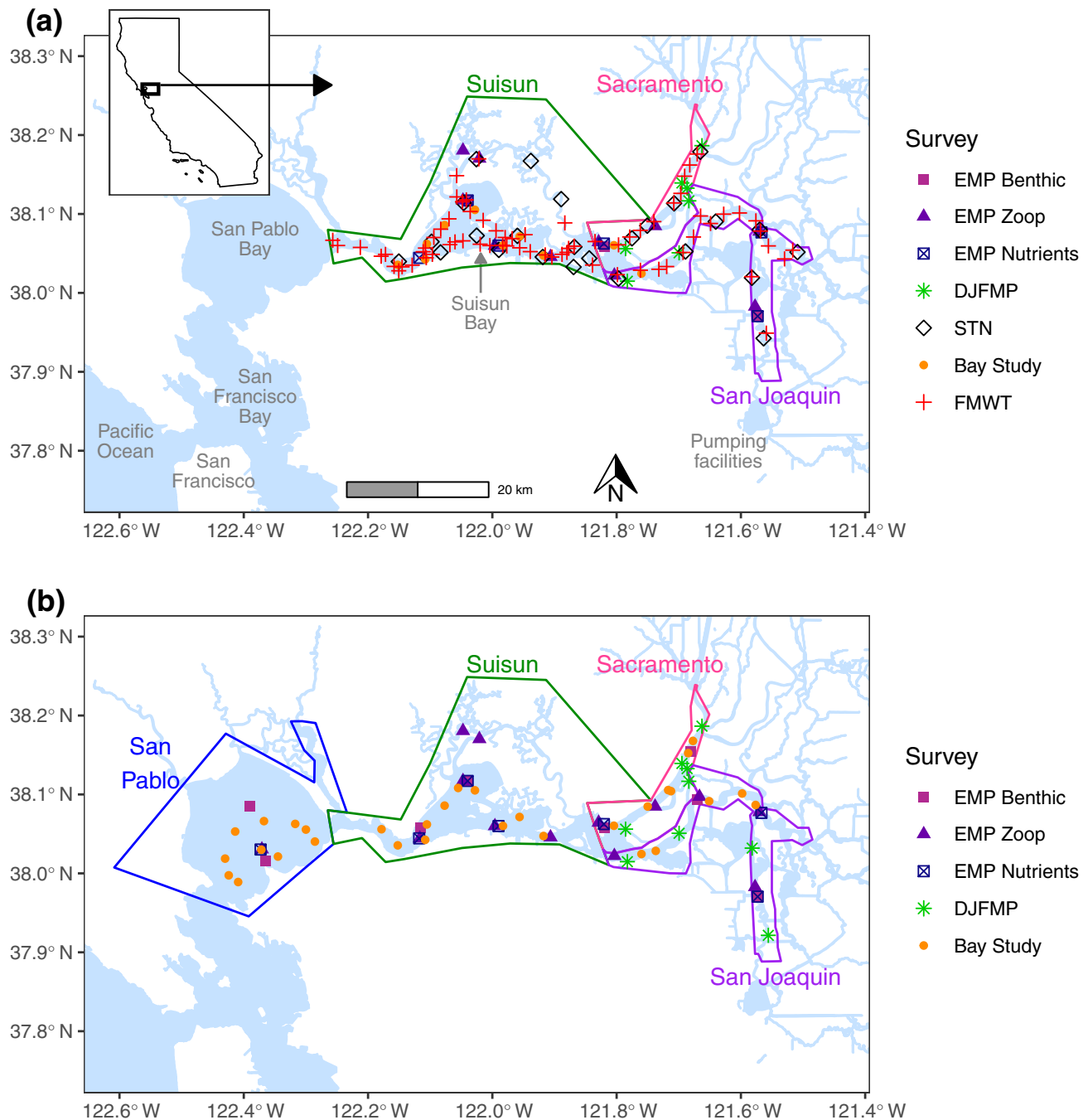
California, while the rest flows downstream toward Suisun Bay, San Pablo Bay, and, eventually, the Pacific Ocean (Figure 1). The delta is managed to remain fresh year-round and only experiences salinity intrusion during extreme drought years, whereas San Pablo and Suisun Bays have more variable salinities. 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 1950 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 (*P. 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

**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)	<a href="https://wildlife.ca.gov/Conservation/Delta/Bay-Study">https://wildlife.ca.gov/Conservation/Delta/Bay-Study</a>
Fish (estuarine fishes)	Fall Midwater Trawl Survey (FMWT)	<a href="https://wildlife.ca.gov/Conservation/Delta/Fall-Midwater-Trawl">https://wildlife.ca.gov/Conservation/Delta/Fall-Midwater-Trawl</a>
	Summer Townet Survey (STN)	<a href="https://wildlife.ca.gov/Conservation/Delta/Townet-Survey">https://wildlife.ca.gov/Conservation/Delta/Townet-Survey</a>
Fish (Mississippi Silverside, centrarchid species)	Delta Juvenile Fish Monitoring Program (DJFMP)	Interagency Ecological Program, McKenzie, et al. (2021)
Chlorophyll-a, Temperature, Secchi depth, Nutrients	Environmental Monitoring Program (EMP Water Quality)	Interagency Ecological Program, Martinez, et al. (2021)
Flow	Dayflow, California Department of Water Resources	<a href="https://data.cnra.ca.gov/dataset/dayflow">https://data.cnra.ca.gov/dataset/dayflow</a>



**FIGURE 1** Map of 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.

[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 time series. We also obtained data on dissolved inorganic

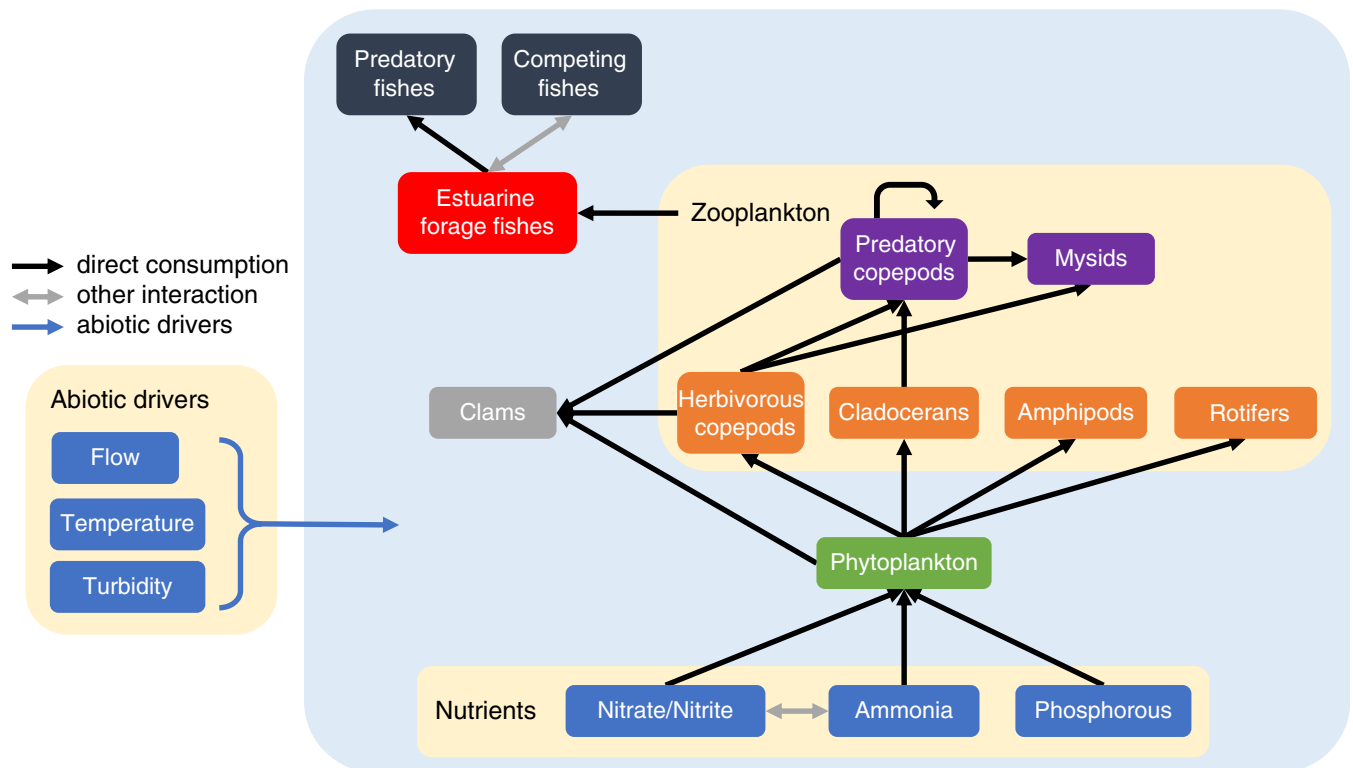
nitrogen (DIN) and three environmental drivers: temperature, flow, and turbidity. Phosphorus was considered but excluded because it is not limiting in the system (Cloern et al., 2020), and salinity was considered but excluded as it is highly correlated with flow in this system. We ensured the methods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

Each variable in each source data set was summarized into annual, annual-regional, and monthly-regional averages (Appendix S1: Figures S1–S5, Table S2), allowing for models with different spatial and temporal resolutions. Both the annual and annual-regional data sets 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 consistently monitored sampling stations (Appendix S1: Table S3). For both annual- and monthly-regional data sets, 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) (Figure 1). Due to limited sampling in

San Pablo before the mid-1990s, this region was only included for the monthly-regional data set.

### Analysis

We evaluated relationships among the food web components and environmental drivers using 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 (Figure 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 spatio-temporal resolution (annual, annual-regional, and monthly-regional) that had a corresponding data set (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 timescales were fit separately to each region. Species were omitted from models of particular regions if they were rare or not sampled in that region.



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

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 data sets (BSMT, FMWT, STN). Environmental drivers and clams were included as exogenous predictors. Contemporaneous values were used for all relationships because of the subannual 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” model (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, which allowed 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 time point. 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. SEMs 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. These models had a large number of parameters relative

to data (Wolf et al., 2013). Thus, a nonsignificant 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: 0.15–0.61). These effects were significant in the whole estuary and in the freshwater Sacramento and San Joaquin (Figure 3). Significant trophic links between phytoplankton and herbivorous zooplankton and between herbivorous and predatory zooplankton were found in the whole estuary, Suisun, and San Joaquin (0.28–0.61). 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 (0.28–0.45).

Turbidity had consistent positive effects on estuarine fishes in all regions (0.26–0.79), 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.

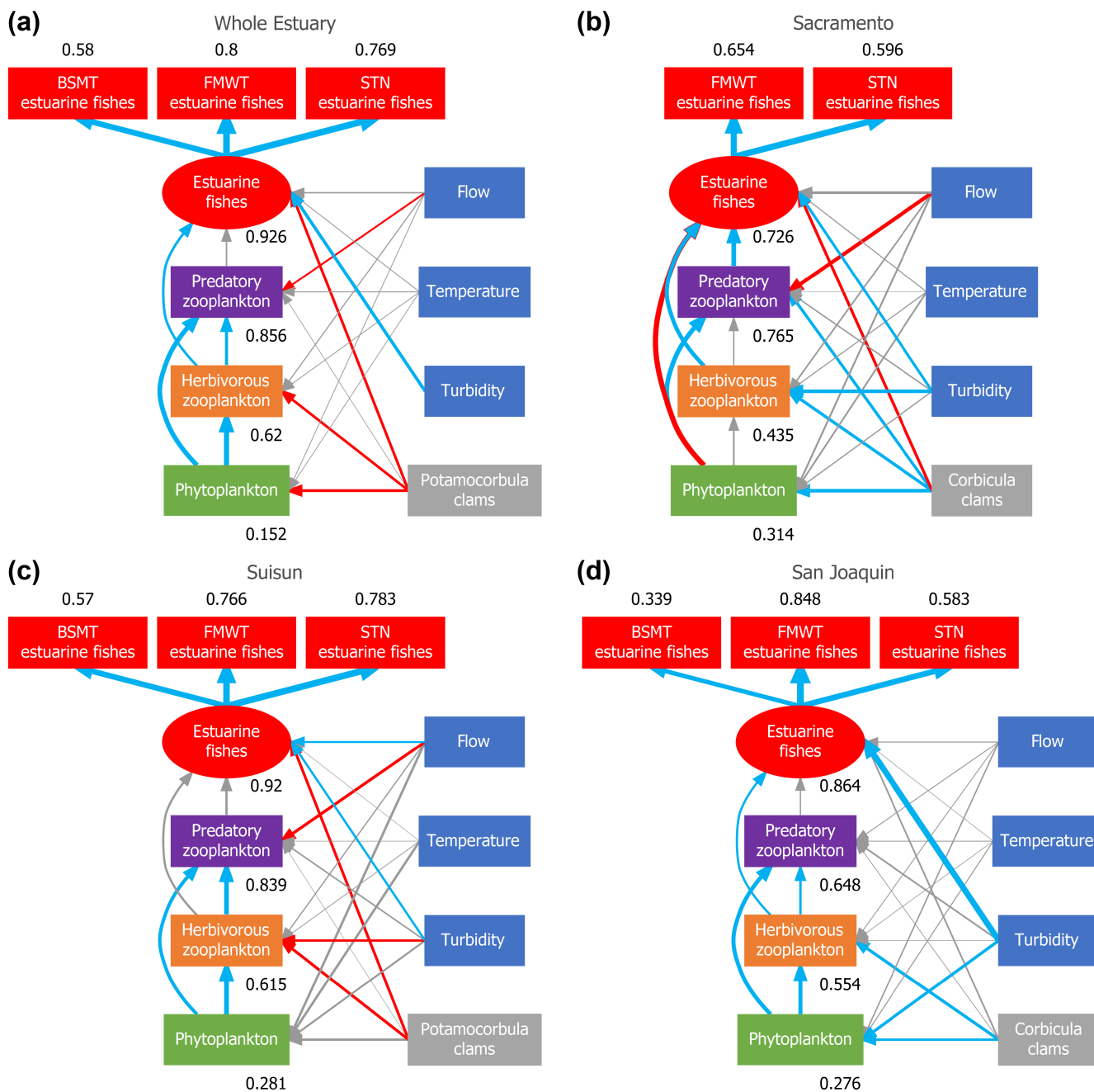
### Monthly-regional models

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

### Annual SEMs

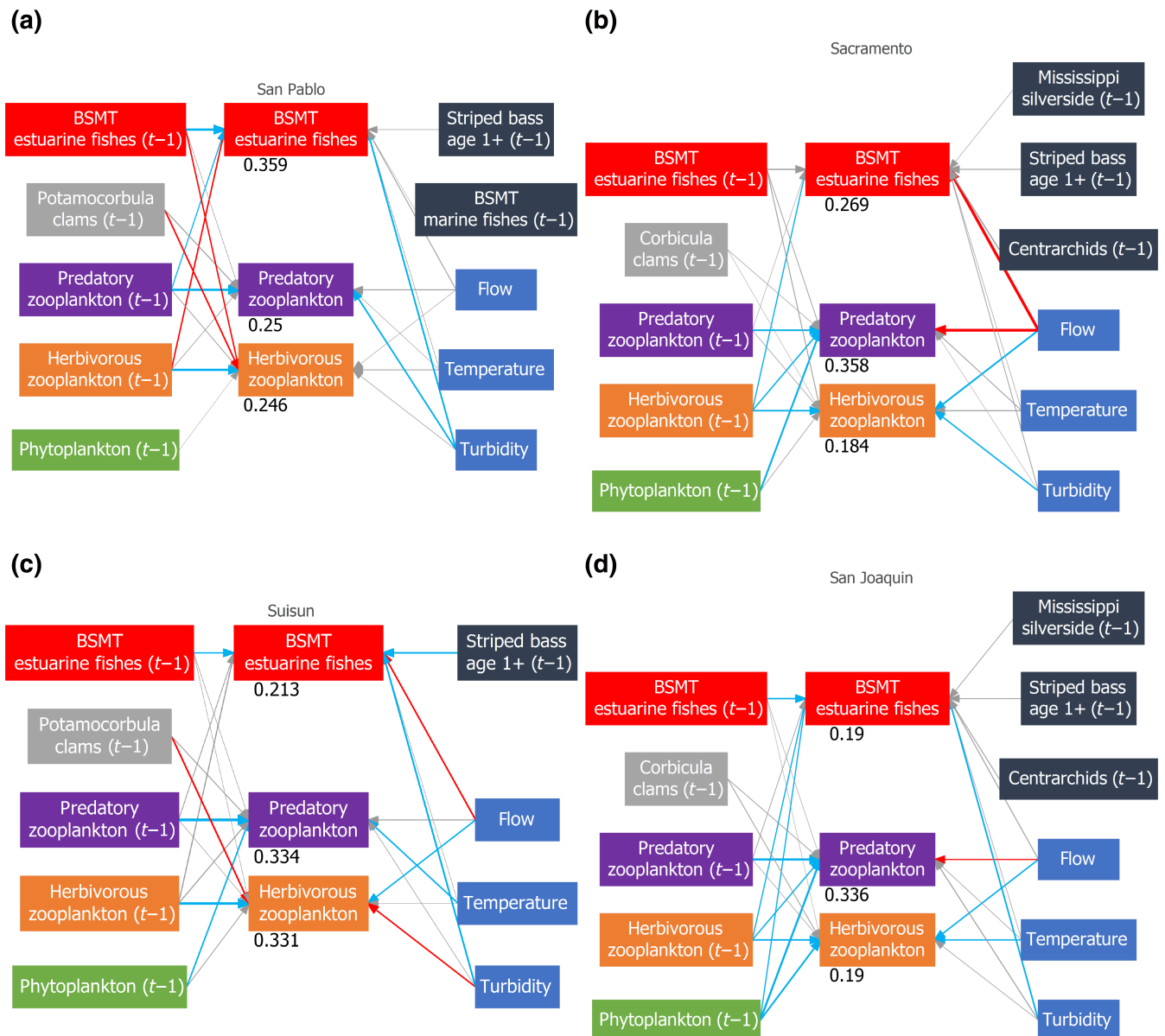


**FIGURE 3** Path diagrams for annual and annual-regional structural equation models. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate coefficients not significantly 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.

effects appeared stronger in the brackish downstream regions (Suisun and San Pablo; Figures 4 and 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 0.13–0.14). Total top-down effects on fishes were only significant in Suisun and Sacramento, although the effect of striped bass was

## Monthly regional models (upper trophic level)



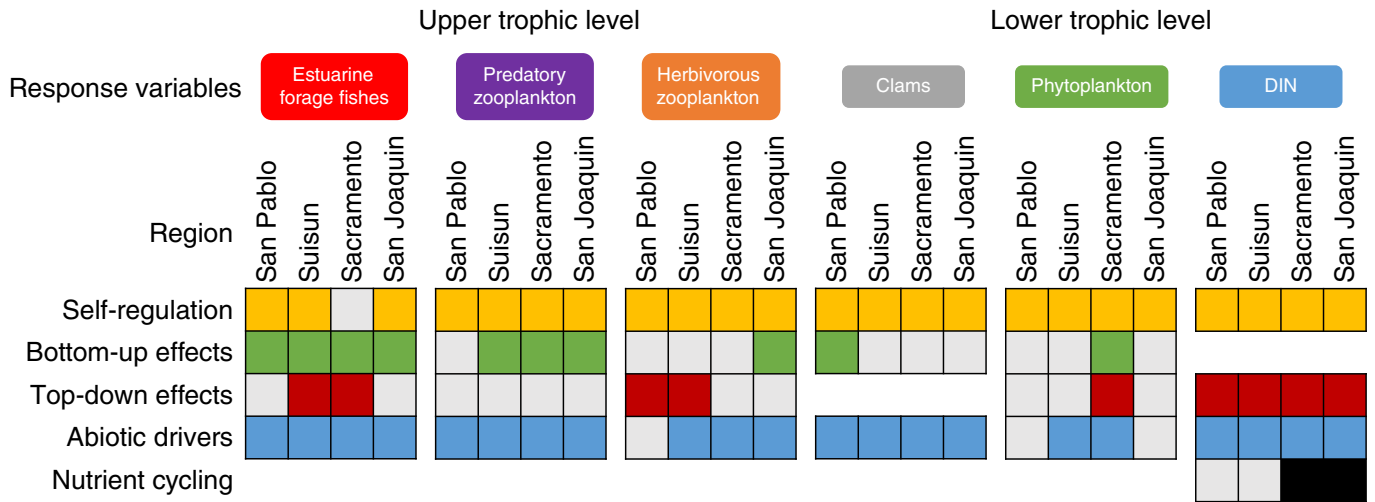
**FIGURE 4** Path diagrams for monthly-regional structural equation models using upper trophic level aggregates. Arrows point from predictor variables to response variables. Blue and red arrows indicate statistically significant positive and negative path coefficients, respectively; gray arrows indicate 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.

positive in Suisun (Figure 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 (Figure 5). The net effect of environmental drivers was typically on par with or greater than bottom-up and top-down effects (Appendix S1: Figure S6a). Consistent with the annual models, turbidity

had a positive effect on fishes in San Pablo, Suisun, and San Joaquin (0.21–0.23; Figure 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).





**FIGURE 5** Summary of total effect sizes for upper trophic level and lower trophic level monthly-regional structural equation models. 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 Appendix S1: Figure S6.

### 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], Figure 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, the 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 (Figure 5). Total environmental effects exceeded total top-down effects for DIN in all regions (Appendix S1: Figure 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 (Appendix S1: Figure S7). The 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.

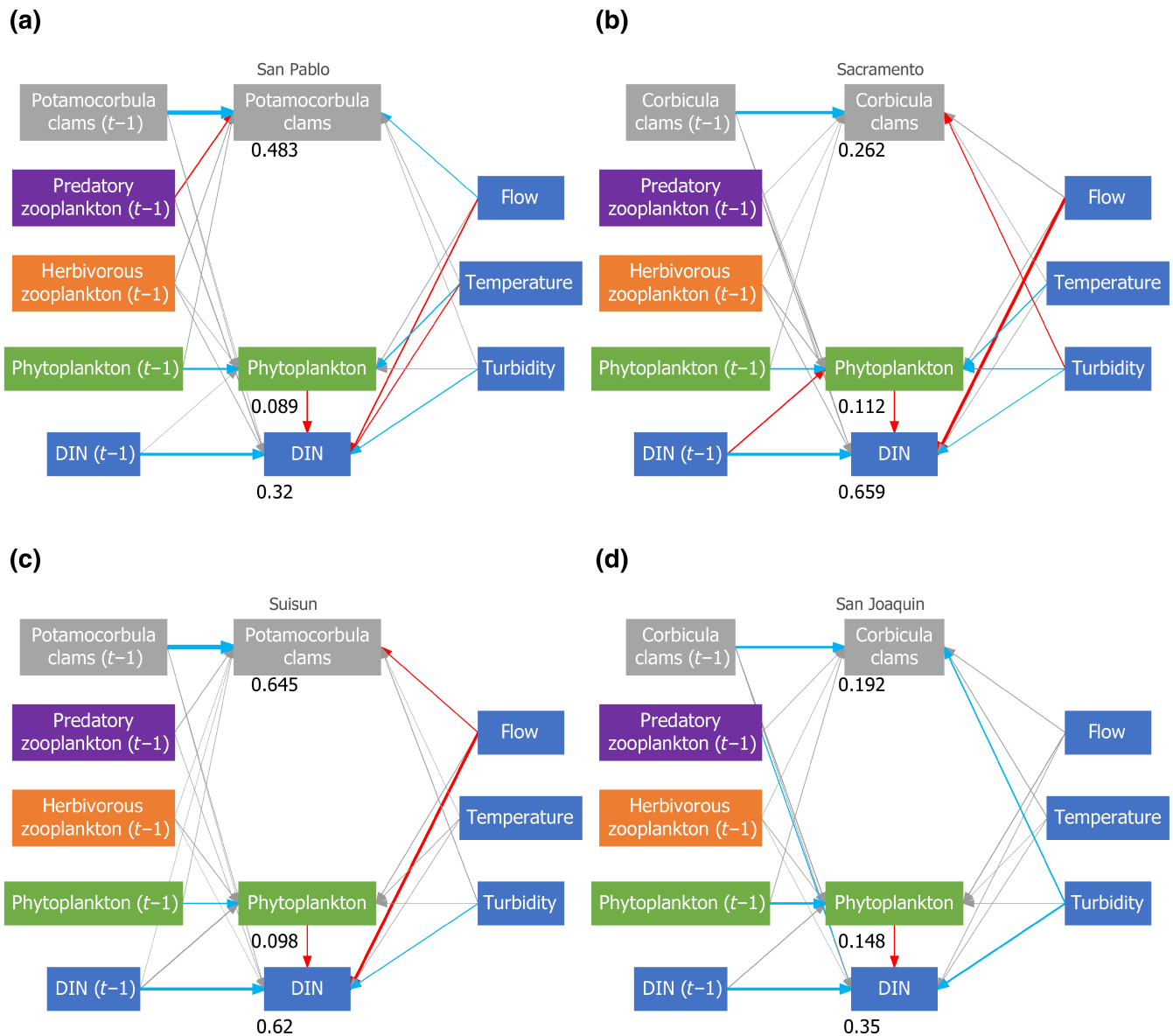
## DISCUSSION

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 varied 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.

### Differences along estuarine gradient

Theoretical and empirical studies have found that greater diversity (Griffin et al., 2013; Srivastava et al., 2009; Ye et al., 2013) and lower productivity (Chase et al., 2000; Oksanen et al., 1981; van de Koppel et al., 1996) can each

## Monthly regional models (lower trophic level)



**FIGURE 6** Path diagrams for monthly-regional structural equation models 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.

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* (Cole et al., 1992; Foe & Knight, 1986). 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.

The 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 could lead to increases in macroalgae, vegetation, and phytoplankton chlorophyll (Woodland et al., 2015), we detected no 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, which 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).

## Timescale effects

A 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.

## Relative strengths of abiotic and biotic drivers

Past studies on zooplankton and forage fishes in estuaries (including the SF Estuary) have found stronger influences of abiotic compared to biotic drivers (Rollwagen-Bollens et al., 2020; Thomson et al., 2010; Wasserman et al., 2022). However, we found net biotic and abiotic effects to be of comparable magnitude. We also found that driver strength varied by region and timescale, in agreement with prior studies that 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 (i.e., flow and turbidity) can often be manipulated directly, for example, through freshwater flow manipulation (Hemraj et al., 2017; Sommer, 2020). To increase the abundance of estuarine fishes and their food supply, this can be easier to implement than biotic interventions such as predator removal.

## Comparison to past studies

With regard to the SF Estuary specifically, our analysis incorporated 12 additional years of data compared to 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 phytoplankton 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.

## Data and modeling limitations

Our study was limited by a lack of regular, long-term monitoring data on several important food web components. For instance, we used chlorophyll-a as a coarse proxy for phytoplankton abundance since we lacked high-quality, long-term phytoplankton data. Although phytoplankton was often a significant driver of zooplankton, phytoplankton 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 time step (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 directions and conclusions

Future work in the SF Estuary might use our food web model and integrated data set (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 that 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 intraspecific 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 data sets 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 in the relationships among productivity, diversity, environmental context, and trophic control within ecosystems.

## AUTHOR CONTRIBUTIONS

Tanya L. Rogers and Samuel M. Bashevkin provided equal contributions.

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## CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT





Data (Mitchell et al., 2023) are available in the Environmental Data Initiative Data Portal at <https://doi.org/10.6073/PASTA/8CB1E3D1312F2034E2345F62EB455403>. Code (Rogers et al., 2024) is available in Zenodo at <https://doi.org/10.5281/zenodo.10552629>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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