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Human-induced biotic invasions and changes in plankton interaction networks

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SUMMARY

1. Pervasive and accelerating changes to ecosystems due to human activities remain major sources of uncertainty in predicting the structure and dynamics of ecological communities. Understanding which biotic interactions within natural multitrophic communities are threatened or augmented by invasions of non-native species in the context of other environmental pressures is needed for effective management.
2. We used multivariate autoregressive models with detailed time-series data from largely freshwater and brackish regions of the upper San Francisco Estuary to assess the connectance, topology, direction and strength of trophic interactions following major invasions and establishment of non-native zooplankton in the early 1990s. We simultaneously compared the effects of fish and clam predation, environmental temperature, and salinity intrusion using time-series data from > 60 monitoring locations and spanning more than three decades.
3. We found changes in the networks of biotic interactions in both regions after the major zooplankton invasions. Our results imply an increased pressure on native herbivores; intensified negative interactions between herbivores and omnivores; and stronger bottom-up influence of juvenile copepods but weaker influence of phytoplankton as a resource for higher trophic levels following the invasions. We identified salinity intrusion as a primary pressure but showed relatively stronger importance of biotic interactions for understanding the dynamics of entire communities.
4. *Synthesis and applications.* Our findings highlight the dynamic nature of biotic interactions and provide evidence of how simultaneous invasions of exotic species may alter interaction networks in diverse natural ecosystems over large spatial and temporal

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scales. Efforts to restore declining fish stocks may be in vain without fully considering the trophic dynamics that limit the flow of energy to target populations. Focusing on multitrophic interactions that may be threatened by invasions rather than a limited focus on responses of individual species or diversity is likely to yield more effective management strategies.

Key-words: Bayesian estimation, conservation of interactions, environmental pressures, estuaries, multivariate autoregressive model, pelagic food webs, time-series.

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INTRODUCTION

Human perturbations of ecosystems range from modifications of the atmosphere and climate to the degradation of habitats through exploitation or introductions of non-native species. These changes directly affect individual species (Walther *et al.* 2002) or taxonomic composition (Winder, Jassby & Mac Nally 2011; Winder & Jassby 2011), but they may also alter the relative importance of biotic interactions within multitrophic networks (Hampton, Scheuerell & Schindler 2006; Francis *et al.* 2012). Networks of biotic interactions are more than the collection of their component species (Montoya, Pimm & Sole 2006) and human perturbations may alter network structure without necessarily affecting species diversity (Tylianakis, Tscharntke & Lewis 2007). Given that biotic interactions affect ecosystem dynamics (McCann, Rasmussen & Umbanhowar 2005), the conservation of network structure recently has been emphasized (McCann 2007; Tylianakis *et al.* 2010), alongside the more traditional foci on individual taxa, community composition or diversity. Changes to interaction networks can transcend biotic boundaries and disrupt ecosystem function, such as biogeochemical cycling (Atwood *et al.* 2013) or distribution of toxic compounds (Stewart *et al.* 2004). Quantifying the strength of biotic interactions modulated by multiple perturbations in diverse natural communities and over large spatial and temporal scales has become a key challenge for community ecology and conservation biology.

Estuaries are complex ecosystems that lie at the interface of ocean, terrestrial and freshwater systems and their biotic communities are adapted to great variation in environmental conditions such as oxygen, temperature and salinity (Elliott & Whitfield 2011). Global threats to estuarine community structure, function and services result from the large fraction of the world's human population living near estuaries (Lotze *et al.* 2006). Releases of ballast water from cargo

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ships may be the world's largest invasion vector that can restructure entire ecosystems (Ruiz *et al.* 1997; Seebens, Gastner & Blasius 2013). Although estuarine communities are adapted to a highly variable environment and therefore potentially resistant to certain anthropogenic pressures (Elliott & Quintino 2007; Elliott & Whitfield 2011), our understanding of their resistance to species invasions is rudimentary.

The San Francisco Estuary is a coastal ecosystem that has been much modified by habitat degradation, water harvesting, increased temperature, and a high ratio of non-native to native species (Cloern & Jassby 2012). This estuary, the largest on the US Pacific coast, provides many ecosystem services and is one of the most biotically invaded estuaries in the world (Cohen & Carlton 1998). A series of invasions over the last four decades caused sharp declines of native zooplankton, shifting species composition to a community resembling that of east-Asian estuaries (Orsi & Ohtsuka 1999; Winder, Jassby & Mac Nally 2011). These taxonomic shifts potentially altered negative (competition, predation) and positive (facilitation) interactions within and among trophic levels, with flow-on effects on food-web structure and dynamics. Previous univariate analyses indicated the negative effects of the invasive bivalve *Potamocorbula amurensis* (hereafter *Potamocorbula*) on phytoplankton, zooplankton, and several fish species (Alpine & Cloern 1992; Cloern 1982; Kimmerer, Gartside & Orsi 1994; Kimmerer 2006). In addition to individual zooplankton invasions, there was a major simultaneous invasion of three non-native copepod species that became established in the early 1990s and that dominated the zooplankton assemblage thereafter (Orsi & Ohtsuka 1999; Winder & Jassby 2011). The impact of such simultaneous invasions on native assemblages is expected to be more severe than if each of the species had invaded and established asynchronously (Simberloff & Von Holle 1999).

Despite the importance and complexity of plankton communities (Hays, Richardson &

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Robinson 2005), the strength of interactions in plankton networks and their changes in human-altered ecosystems remain poorly understood. In the upper San Francisco Estuary, in situ interactions among plankton taxa have not been explored systematically in a multivariate framework. A single study quantified strengths of trophic interactions among pelagic fishes and two groups of calanoid copepods (Mac Nally *et al.* 2010). However, that study did not explore interaction strengths among all zooplankton and phytoplankton functional groups and included only chlorophyll-*a* as a proxy for total phytoplankton biomass.

Here, we focus on interactions among major phytoplankton and zooplankton functional groups and relate these to pelagic fish biomass, seawater temperature, salinity intrusions and biotic invasions. We employed detailed monitoring data sets for pelagic fish, zooplankton and phytoplankton to compare the topology, directions, and strength of trophic interactions before and after the establishment of non-native zooplankton (hereafter 'pre-invasion' and 'post-invasion' period respectively). We analyzed the shift in the interaction network from the pre-invasion period (1974–1992) to the post-invasion period (1993–2008) and the relative influence of key covariates using multivariate autoregressive (MAR) models (Ives *et al.* 2003). Our specific goal was to explore whether, and how, the shifts in relative abundances of plankton taxa (Winder & Jassby 2011) after the establishment of non-native copepods around 1993 altered the importance of trophic interactions among the major plankton functional groups. We predicted shifts in biotic interactions after the establishment of invasive zooplankton species. In particular, we expected to detect stronger interactive effects of invasive predators and weaker effects of native herbivores because of major abundance shifts within these functional groups (Winder & Jassby 2011). We also predicted that salinity intrusions and the bivalves will influence plankton interaction network as previous analyses showed these variables can strongly alter dynamics of

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individual plankton groups (Kimmerer, Gartside & Orsi 1994, Jassby *et al.* 1995). We show that species invasions could potentially modify the connectance and topology of interaction networks and highlight the importance of changes to biotic interactions when designing effective conservation and management strategies.

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MATERIALS AND METHODS

We focused our analysis on the upper San Francisco Estuary consisting of the brackish, low-salinity Suisun Bay and Marsh (hereafter 'Suisun region') and largely freshwater inverted delta formed by Sacramento and San Joaquin rivers (hereafter 'delta region'). These two regions have been a great focus of natural resource management where major functional groups of the community and environmental covariates have been monitored for more than three decades. We analyzed both regions separately, as they differ in their abiotic conditions and the community composition (Winder & Jassby 2011), and we wished to compare the responses of interaction networks to species invasions in each of them. All data included in this study (http://www.water.ca.gov/iep/) were collected at discrete sampling sites in the upper San Francisco Estuary by the California Department of Fish and Wildlife (DFW) as part of the Interagency Ecological Program (IEP) between 1974 and 2008.

Response variables and covariates

Zooplankton biomass

Zooplankton samples were collected using oblique tow nets (154 µm mesh size) or pumped through a 64 µm mesh, bi-weekly or monthly (for details of the methods see Orsi & Mecum 1986). We converted zooplankton densities to carbon biomass and calculated annual means (Winder & Jassby 2011) to capture shifts in the long-term biomass of key functional groups (Fig. 1). We used time-series data from six consistently sampled locations in Suisun and from seven consistently sampled locations in the delta.

Zooplankton taxa and their life stages were classified by their feeding function into five major groups: nauplii, herbivores, omnivores, small predators and predators. Nauplii are larval

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stages of copepods and are also an important food for omnivorous and predatory zooplankton, clams, and larval fish. Herbivores are suspension feeders consuming phytoplankton. They can compete with, or serve as food for, other zooplankton groups. Herbivores include native cladocerans, such as *Daphnia* spp., *Bosmina* spp., *Diaphanosoma* spp., and rotifers such as *Asplanchna* spp., *Keratella* spp., *Polyarthra* spp., *Synchaeta* spp. and *Trichocerca* spp. Omnivores feed on phytoplankton, suspended particulate matter, and smaller zooplankton including their juvenile stages; omnivores include three probably native species of *Acartia* spp., *Eurytemora affinis*, and introduced *Pseudodiaptomus* spp., and *Sinocalanus doerrii*. We characterize the group 'small predators' as zooplankton of smaller sizes (< 500 µm) that likely derive carbon from the microbial pool, feeding on ciliates, flagellates, and some taxa also on detritus and bacteria. This group is composed largely of introduced cyclopoids *Limnoithona* spp., and *Oithona davisae*, and harpacticoids. The 'predators' include native *Acanthocyclops* spp. and introduced *Acartiella sinensis* and *Tortanus dextrilobatus* which can reach ten times the individual body mass of the 'small predators' (Gould & Kimmerer 2010). This group is at the top of the planktonic food web, largely feeding on other zooplankton species (Hooff & Bollens 2004; York *et al.* 2013).

Phytoplankton biovolume

The phytoplankton samples were collected with a submersible pump from 1 m depth. We used phytoplankton abundance data from three locations in Suisun and three locations in the delta region that have been sampled consistently. To obtain an estimate of phytoplankton biovolumes, we used median values from direct measurements (IEP) or from published literature, and applied median biovolumes for individual phytoplankton taxa to the entire time-series (Fig. 2). Despite

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the simplification of using median values, biovolume data provide information on taxonomic composition and food quality, which greatly affect resource availability for zooplankton, and consequently is a better proxy of resource availability than chlorophyll-*a*. We aggregated the data into high-quality (cryptomonads and diatoms) and low-quality (other taxa including cyanobacteria, dinoflagellates, green algae, chrysophytes, euglenoids, synurophytes and haptophytes) groups (Brett, Müller-Navarra & Park 2000).

Biotic and abiotic covariates

We quantified the relative influence of four covariates that are predicted to have substantial effects on plankton groups and potentially on their interactions. Two biotic covariates were: summed biomass of the five dominant planktivorous fish species (northern anchovy *Engraulis mordax*, American shad *Alosa sapidissima*, threadfin shad *Dorosoma petenense*, age-0 striped bass *Morone saxatilis,* and longfin smelt *Spirinchus thaleichthys*); and the abundance of an invasive suspension-feeding bivalve, *Potamocorbula amurensis*. Fish samples were collected each month from September to December as a part of the Fall Midwater Trawl Survey conducted by the California Department of Fish and Wildlife (DFW). Fish data were derived from 42 locations that were sampled every year over the entire time-series and converted to biomass (mg C m^{-3}) using length-weight regression functions (Kimmerer *et al.* 2005). Most of the fish collected in this program are young-of-the-year planktivores (median lengths from 70 to 81 mm from September to December) and their biomass can therefore be used as an index of planktivorous fish biomass throughout the year. *Potamocorbula* spread rapidly across the low-salinity Suisun region after its introduction in 1986 (Alpine & Cloern 1992), but is not abundant in largely freshwater parts of the delta. The bivalve data were derived from two locations (D4-L

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and D7-C) that were sampled the same sampling period. Two abiotic covariates were annual means of surface temperature, recorded at the same locations and time as the zooplankton samples were collected, and the distance from the mouth of the estuary of the daily-averaged, near-bottom salinity of 2 (practical salinity scale), locally termed 'X_2' (Jassby *et al.* 1995). X_2 is a synthetic measure of the physical responses of the estuary to freshwater flow (Monismith *et al.* 2002).

Statistical methods

We used a variant of a multivariate, autoregressive model (MAR; Ives *et al.* 2003; Supporting Information) to analyze the dynamics of plankton functional groups. The MAR method was developed to estimate ecological interactions from time-series data and has been applied to plankton interaction networks in freshwater (e.g., Ives *et al.* 2003; Hampton, Scheuerell & Schindler 2006) and marine (e.g., Francis *et al.* 2012) ecosystems. We built separate MAR models for each region, which included time-dependent parameters that tested for differences in intra-specific interactions and covariate effects between the pre- (1974-1992) and post- (1993-2008) invasions periods. The Bayesian framework allowed us to incorporate our prior expectations for the direction of biotic interactions and the effects of main covariates. We used normal prior distributions with unit variance and means that reflected prior expectations for the direction of influence, i.e. $N(\mu\ 1)$, with μ = -0.675, +0.675 and 0 for parameters with negative, positive, or unknown prior expectations, respectively (Mac Nally *et al.* 2010). Parameters quantifying changes in intra-specific interactions or covariate effects were assigned uninformative, standard normal prior distributions, $N(0,1)$. The informative normal priors corresponded to prior odds of 3:1 in favour of the expected direction of influence (Mac Nally *et*

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al. 2010); uninformative ($\mu=0$) priors correspond to odds of 1:1. We inferred the importance of model parameters from odds ratios (OR, the ratios of posterior odds to prior odds) that parameters were positive or negative. Odds ratios are calculated as $OR = p_1/(1-p_1) : p_0/(1-p_0)$, where p_1 and p_0 are the posterior and prior probabilities, respectively, that the parameter is positive (or negative). If the OR $\geq$ 3.2, we concluded that there was substantial support in the data for the expected relationship. If 1 $\leq$ OR < 3.2, the data did not invalidate the expectation but there was relatively little support (Jeffreys 1961). We used hierarchical partitioning to determine the relative importance of autoregressive terms, among- plankton interactions, and covariate effects in explaining the variation in data in each region (see Supporting Information for details).

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RESULTS

Our MAR models for the two regions fitted the time-series data well, as gauged by $R^2 = 0.894$ for Suisun and $R^2 = 0.892$ for the delta. The among-functional group components of the models were most important in explaining variation in the data for both regions, followed by the covariates and then the autoregressive components. Ratios for the hierarchical partitioning of the explained variance were 1 : 0.77 : 0.35 in Suisun and 1 : 0.43 : 0.04 in delta, indicating that trophic interactions among the functional groups are likely to be the key determinant of the plankton community dynamics.

Relationships in the Suisun region

There appeared to be differences in the importance of biotic interactions and environmental covariates in the pre-invasion and post-invasion time periods in Suisun (Fig. 3, Table 1). Prior to the 1993 invasions, the biomass of omnivores was positively correlated with phytoplankton, especially with high-quality food taxa, and negatively correlated with predators (Fig. 3a). The association between omnivores and phytoplankton was not evident after 1993. Instead, we found negative reciprocal correlations between omnivore and herbivore biomasses (Fig. 3b). Both omnivores and herbivores were negatively associated with X_2 and predator biomass in the post-invasion Suisun (Fig. 3b). Predator biomass was positively associated with omnivore biomass after 1993, but not before (Fig 3). There was some evidence of reciprocal positive associations between omnivores and nauplii after 1993, but these relationships had weak support (OR = 2.9). There was no evidence of omnivore-nauplii associations before 1993. Biomasses of copepod nauplii were negatively related to *Potamocorbula* abundance, and low-quality phytoplankton was negatively related to X_2 before, but not after, the invasions in 1993 (Fig. 3).

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We analyzed the temporal changes in the direction and strength of the relationships between 1974–1992 and 1993–2008 (see strongly supported deviations in Table 1). In the latter period there was a shift toward negative correlation between omnivores and herbivores, an increased negative effect of predators on herbivores and an increased positive effect of nauplii on omnivores. We found a weakening of the negative effect of *Potamocorbula* on nauplii and a strengthening of the negative effects of X_2 on herbivores and omnivores after 1993 (Table 1).

Relationships in the delta region

There were fewer correlations among plankton functional groups, and fewer relationships between plankton and environmental covariates in the delta region than in Suisun (Fig. 4, Table 1). We did not find any associations between phytoplankton or nauplii and other zooplankton groups in either time period, and all correlations among plankton groups in the delta were negative. In the pre-invasion delta, there was strong support for negative effects of predators on herbivores, small predators on nauplii, and omnivores on small predators (Fig. 4a). Nauplii were positively correlated with X_2 before 1993 (Fig. 4a). None of these relationships was evident in the delta after 1993.

In the post-invasion delta, predators were positively associated with X_2, while herbivores were negatively associated with omnivore biomass (Fig. 4b). This last coefficient had marginal support (OR = 3.1). Direct comparison of model parameters for the pre- and post- invasion periods (deviations in Table 1) suggest reduced influence of small predators and X_2 on nauplii, and an increase in the positive effect of X_2 on predators.

There was little evidence to suggest that pelagic fish or water temperature affected the plankton communities in either region or time period (Figs 3, 4).

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DISCUSSION

Our study indicates substantial changes in the strength and direction of interactions among the plankton functional groups following the establishment of invasive copepods in the upper San Francisco Estuary in the early 1990s. Among the strongest shifts were negative reciprocal correlations between omnivores and herbivores in the post-invasion Suisun that were not evident before the invasions. These findings are consistent with intensified competition for the reduced phytoplankton resource in this region. Introduced omnivorous *Pseudodiaptomus* spp. (Orsi & Walter 1991; Winder & Jassby 2011) probably contributed to the negative effects of omnivores on herbivores. A shift toward a stronger negative effect of predators on herbivores in the post-invasion Suisun probably arose from predation by invasive *A. sinensis* and *T. dextrilobatus* after their establishment around 1993 (Orsi & Ohtsuka 1999), while salinity intrusions likely mediated these relationships. Herbivores, mainly consisting of rotifers in Suisun and cladocerans and rotifers in the delta, declined sharply and our analysis suggests that competition and predation from other zooplankton groups may have contributed to this decline, although ammonium discharge (Dugdale *et al.* 2007) and other introductions (e.g., Kimmerer & Orsi 1996) were likely contributing factors.

The biomass of omnivorous zooplankton was positively associated with phytoplankton in the pre-invasion Suisun, but with nauplii in the recent post-invasion period. The association between nauplii and omnivores indicates copepod recruitment since the omnivores' principal food is microzooplankton such as ciliates (York *et al.* 2013), which are not sampled by the monitoring programs. A decline in phytoplankton and an increase in nauplii biomass after invasions (Winder & Jassby 2011) reduced the importance of phytoplankton as a food resource. Such changes in the interactions between primary producers and zooplankton consumers that

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form the food sources for pelagic fish can greatly alter energy transfer to higher trophic levels (Ravet, Brett & Arhonditsis 2010). The absence of correlations between herbivores and phytoplankton in both regions indicates that other processes than mesozooplankton grazing may control phytoplankton dynamics (Kimmerer 2006; Kimmerer & Thompson 2014). A meta-analysis of observational and experimental studies from marine pelagic ecosystems showed similar loose coupling between zooplankton and phytoplankton biomasses (Micheli 1999).

We expected to detect competitive effects of *L. tetraspina* on other groups because after 1993 this small predator became the numerically dominant in Suisun. However, 'small predators' appeared to have little association with other plankton groups. *L. tetraspina* feeds preferentially on protists, but rarely consumes diatoms (Bouley & Kimmerer 2006) and it is too small to consume calanoid copepods. Our results are consistent with laboratory experiments (Bouley & Kimmerer 2006) and suggest that *L. tetraspina* may not compete with or prey upon native zooplankton groups. The negative effect of small predators on nauplii in the delta declined after the establishment of *L. tetraspina* in 1993 in an agreement with this species being a source rather than a consumer of nauplii. Nevertheless, *Limnoithona* spp. may be a resource for predatory zooplankton (York *et al.* 2013). The weakening of the negative correlation between predators and herbivores after 1993 in the delta region is consistent with a shift from the native predators *Acanthocyclops* spp. to invasive *A. sinensis.*

In general, there were fewer statistically important associations and the shift in the plankton network structure was less apparent in the delta region than in Suisun. This may be due to the different taxonomic composition of individual functional groups and the lower densities of predatory copepods established in the delta after 1993. Furthermore, plankton dynamics can be more strongly driven by the changes in the freshwater flow, water clarity, and ammonium

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discharges in the delta than in the Suisun region. Greater strengths and numbers of potential negative interactions in Suisun than in the delta suggests that changes in a particular functional group, such as nauplii, could potentially cascade to other components of food webs.

Our results suggest a strong effect of the isohaline index X_2 on community structure in both regions, which has been reported elsewhere (Jassby *et al.* 1995; Mac Nally *et al.* 2010; Winder, Jassby & Mac Nally 2011). Given that X_2 represents principally the response of the salinity field to freshwater flow into the estuary, and species are distributed spatially along a salinity gradient, association with X_2 can be understood as a consequence of interannual movement of the plankton across the delta – Suisun boundary. X_2 in the post-invasion Suisun was negatively correlated with herbivores and omnivores that may have narrow salinity ranges (e.g., Kimmerer 2002). When freshwater flow increases the delta regions goes from being mostly fresh to entirely fresh, while Suisun region can go from being entirely brackish to largely fresh for much of the year. This potentially underlies some, though not all, of the observed interactions among functional groups and results in differential patterns in both regions.

Prior studies have documented a negative effect of *Potamocorbula* on phytoplankton, copepod nauplii, and individual species of zooplankton and fish (Alpine & Cloern 1992; Kimmerer, Gartside & Orsi 1994; Kimmerer 2006). Our study suggests a negative effect of *Potamocorbula* on nauplii in Suisun before 1993, where relatively high nauplius biomass sharply declined soon after the introduction of *Potamocorbula* in 1986 (see also Kimmerer, Gartside & Orsi 1994). Nauplii did not appear to be negatively affected by the clam after 1993, but increased due to the recruitment of new invasive zooplankton, mainly *Limnoithona* spp. (Winder & Jassby 2011). The lack of response of plankton to *Potamocorbula* abundance in our study may relate to

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the highly variable size of clams, and therefore a weak relationship between their numerical abundance and grazing rate.

Other covariates appeared to have little effect on plankton community structure in both regions. Abundance of fish was unrelated to zooplankton community dynamics, which is obvious also from the independent dynamics of these groups after a steep drop in production of pelagic fish in the early 2000s (Thomson *et al.* 2010). We found no evidence that water temperature affected the plankton community, but other temperature-related variables, such as variability or the frequency of extreme temperatures, may be also relevant and warrant further investigations.

The MAR framework is well suited to explore links among functional groups and to investigate the responses of ecological communities to perturbations in a multivariate framework (Ives *et al.* 2003; Mac Nally *et al.* 2010; Francis *et al.* 2012). Although the positive or negative associations among species may indicate biotic interactions, the MAR analyses rely on correlations and cannot inform the causality of these relationships. We assigned the prior expectations to the relationships based on the assumed trophic interactions before the analyses. Despite the weak influence of the priors, few significant relationships showed opposite directions, so that our findings are largely consistent with the previous knowledge about the system.

We used time-series data aggregated annually and across large geographical areas (about 1000 km^2) to remove the effect of seasonal events (e.g., Micheli 1999) and to focus our analysis on long-term trends of plankton dynamics across the regions. Therefore, some short-term or locally important interactions may not have been detected. The MAR analysis assumes linear relationships (on the log-scale), so any non-linear relationships may not have been revealed (Ives *et al.* 2003). Despite these limitations, our results suggested several relationships, some

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previously identified but some new, among plankton functional groups and environmental covariates.

The establishment of three dominant zooplankton species around 1993 was not an isolated event and individual invasions have occurred throughout the time-series. Nevertheless, this simultaneous establishment of invasive copepods was followed by major shifts in the relative species abundance within the functional groups and in the relative importance of the functional groups within the entire plankton community (Winder, Jassby & Mac Nally 2011; Winder & Jassby 2011). Our results imply that these changes, in combination with other human-induced perturbations, have the potential to modify the network of biotic interactions. We identified that herbivores are the functional group most affected by negative interactions and their loss may have cascading effects on biodiversity, in particular in the Suisun region. This system likely shifted towards a nutritionally inferior phytoplankton and detrital-based food web, with potential nutritional consequences for secondary consumers. The importance of some environmental covariates shifted between the two time periods, although there appeared to be a relatively stronger influence of biotic interactions than any of the covariates.

There are few studies that investigate changes in the biotic network structure following invasions of non-native species. Recent exceptions that focused on the complex plant–pollinator networks in terrestrial systems found no effect of invasive species on overall connectance (the number of realized links relative to the number of possible links; Aizen, Morales & Morales 2008; Heleno *et al.* 2009), but the connectance among native species declined (Aizen, Morales & Morales 2008). Our analysis of a simplified network among plankton functional groups suggests that connectance can either increase (Suisun) or decline (delta), following the invasions (Figs 3,

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4). Such different responses highlight the importance of understanding the environmental context when assessing the impacts of invasive species on community structure (Tylianakis *et al.* 2008).

There is increasing recognition of the importance of altered trophic interactions and energy flows in ecosystems degraded by human activities (e.g., Naiman *et al.* 2012). Attempts to restore individual taxa or diversity may be in vain if altered trophic dynamics limit the flow of energy to target populations. Our results suggest that the planktonic food web in Suisun, in particular, may have been fundamentally altered following zooplankton invasions. Such changes probably alter the flows of energy and resource flows to higher trophic levels, and, therefore, have implications for understanding or reversing recent declines in fish populations in this system.

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REFERENCES

Aizen, M.A., Morales, C.L. & Morales, J.M. (2008) Invasive mutualists erode native pollination webs. *Plos Biology,* **6,** 396-403.

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

Atwood, T., Hammill, E., Greig, H.S., Kratina, P., Shurin, J.B., Srivastava, D.S. & Richardson, J.S. (2013) Predator-induced reduction in freshwater carbon dioxide emissions. *Nature Geoscience*, **6,** 191-194.

Bouley, P. & Kimmerer, W.J. (2006) Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. *Marine Ecology Progress Series,* **324,** 219-228.

Brett, M.T., Muller-Navarra, D.C. & Park, S.K. (2000) Empirical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. *Limnology and Oceanography,* **45,** 1564-1575.

Chauvaud, L., Thompson, J.K., Cloern, J.E. & Thouzeau, G. (2003) Clams as CO2 generators: The Potamocorbula amurensis example in San Francisco Bay. *Limnology and Oceanography,* **48,** 2086-2092.

Cloern, J.E. (1982) Does the benthos control phytoplankton biomass in south San Francisco Bay (USA)? *Marine Ecology Progress Series,* **9,** 191-202.

Cloern, J.E. & Jassby, A.D. (2012) Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay. *Reviews of Geophysics*, **50,** 1-33.

Cohen, A.N. & Carlton, J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science,* **279,** 555-558.

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

Elliott, M. & Quintino, V. (2007) The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin,* **54,** 640-645.

Elliott, M. & Whitfield, A.K. (2011) Challenging paradigms in estuarine ecology and management. *Estuarine Coastal and Shelf Science,* **94,** 306-314.

Francis, T.B., Scheuerell, M.D., Brodeur, R.D., Levin, P.S., Ruzicka, J.J., Tolimieri, N. & Peterson, W.T. (2012) Climate shifts the interaction web of a marine plankton community. *Global Change Biology,* **18,** 2498-2508.

For Peer Review

Gould, A. & Kimmerer, W. (2010) Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in upper San Francisco Estuary. *Marine Ecology Progress Series,* **412,** 163–177.

Hampton, S.E., Scheuerell, M.D. & Schindler, D.E. (2006) Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography,* **51,** 2042-2051.

Hays, G.C., Richardson, A.J. & Robinson, C. (2005) Climate change and marine plankton. *Trends in Ecology & Evolution,* **20,** 337-344.

Heleno, R.H., Ceia, R.S., Ramos, J.A. & Memmott, J. (2009) Effects of Alien Plants on Insect Abundance and Biomass: a Food-Web Approach. *Conservation Biology,* **23,** 410-419.

Hooff, R.C. & Bollens, S.M. (2004) Functional response and potential predatory impact of Tortanus dextrilobatus, a carnivorous copepod recently introduced to the San Francisco Estuary. *Marine Ecology Progress Series,* **277,** 167-179.

Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003) Estimating community stability and ecological interactions from time-series data. *Ecological Monographs,* **73,** 301-330.

Jassby, A.D., Kimmerer, W.J., Monismith, S.G., Armor, C., Cloern, J.E., Powell, T.M., Schubel, J.R. & Vendlinski, T.J. (1995) Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications,* **5,** 272-289.

Jeffreys, H. (1961) *Theory of probability*. Oxford University Press, Oxford.

Kimmerer, W.J. (2002) Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series,* **243,** 39-55.

Kimmerer, W.J. (2006) Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. *Marine Ecology Progress Series,* **324,** 207-218.

Kimmerer, W.J., Avent, S.R., Bollens, S.M., Feyrer, F., Grimaldo, L.E., Moyle, P.B., Nobriga, M. & Visintainer, T. (2005) Variability in length-weight relationships used to estimate biomass of estuarine fish from survey data. *Transactions of the American Fisheries Society,* **134,** 481-495.

Kimmerer, W.J., Gartside, E. & Orsi, J.J. (1994) Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San-Francisco Bay. *Marine Ecology Progress Series,* **113,** 81-93.

Kimmerer, W.J. & Orsi, J.J. (1996) Changes in the zooplankton of the San Franscisco Bay Estuary since the introduction of the clam *Potamocorbula amurensis*. *San Francisco Bay: The eosystem* (ed. J.T. Hollibaugh), pp. 403-424. San Francisco: Pacific Division of the American Association for the Advancement of Science.

For Peer Review

Kimmerer, W.J. & Thompson, J.K. (2014) Phytoplankton growth balanced by clam and zooplankton grazing and net transport into the low-salinity zone of the San Francisco Estuary. *Estuaries and Coasts,* doi10.1007/s12237-013-9753-6.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. & Jackson, J.B.C. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science,* **312,** 1806-1809.

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

McCann, K. (2007) Protecting biostructure. *Nature,* **446,** 29-29.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters,* **8,** 513-523.

Micheli, F. (1999) Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science,* **285,** 1396-1398.

Monismith, S.G., Kimmerer, W., Burau, J.R. & Stacey, M.T. (2002) Structure and flow-induced variability of the subtidal salinity field in northern San Francisco Bay. *Journal of Physical Oceanography,* **32,** 3003-3019.

Montoya, J.M., Pimm, S.L. & Sole, R.V. (2006) Ecological networks and their fragility. *Nature,* **442,** 259-264.

Müller-Navarra, D.C., Brett, M.T., Liston, A.M. & Goldman, C.R. (2000) A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature,* **403,** 74-77.

Naiman, R.J., Alldredge, J.R., Beauchamp, D.A., Bisson, P.A., Congleton, J., Henny, C.J., Huntly, N., Lamberson, R., Levings, C., Merrill, E.N., Pearcy, W.G., Rieman, B.E., Ruggerone, G.T., Scarnecchia, D., Smouse, P.E. & Wood, C.C. (2012) Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the United States of America,* **109,** 21201-21207.

Orsi, J.J. & Mecum, W.L. (1986) Zooplankton distribution and abundance in the Sacramento-San-Joaquin Delta in relation to certain environmental-factors. *Estuaries,* **9,** 326-339.

Orsi, J.J. & Ohtsuka, S. (1999) Introduction of the Asian copepods *Acartiella sinensis, Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. *Plankton Biology Ecology,* **46,** 128-131.

For Peer Review

Orsi, J.J. & Walter, T.C. (1991) *Pseudodiaptomus forbesi* and *P. marinus* (Copepoda: Calanoida), the latest Copepod immigrants to California's Sacramento-San Joaquin Estuary. *Proceedings of the Fourth International Conference on Copepods; Bull. Plankton Soc. Japan, Special Vol.,* **1991,** 553-556.

Ravet, J.L., Brett, M.T. & Arhonditsis, G.B. (2010) The effects of seston lipids on zooplankton fatty acid composition in Lake Washington, Washington, USA. *Ecology,* **91,** 180-190.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D. & Hines, A.H. (1997) Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist,* **37,** 621-632.

Seebens, H., Gastner, M.T. & Blasius, B. (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters,* **16,** 782-790.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Stewart, A.R., Luoma, S.N., Schlekat, C.E., Doblin, M.A. & Hieb, K.A. (2004) Food web pathway determines how selenium affects aquatic ecosystems: A San Francisco Bay case study. *Environmental Science & Technology*, **38**, 4519-4526.

Thomson, J.R., Kimmerer, W.J., Brown, L.R., Newman, K.B., Mac Nally, R., Bennett, W.A., Feyrer, F. & Fleishman, E. (2010) Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecological Applications*, **20**,1431-1448.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.

Tylianakis, J.M., Laliberte, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation,* **143,** 2270-2279.

Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature,* **445,** 202-205.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature,* **416,** 389-395.

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

Winder, M., Jassby, A.D. & Mac Nally, R. (2011) Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. *Ecology Letters,* **14,** 749-757.

For Peer Review

York, J.K., McManus, G.B., Kimmerer, W., Slaughter, A.M. & Ignoffo, T.R. (2013) Trophic links in the plankton in the low salinity zone of a large temperate estuary: top-down effects of introduced copepods. *Estuaries and Coasts*, doi10.1007/s12237-013-9698-9.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supporting methods.

For Peer Review

Table 1. Statistical comparison of major biotic interactions and covariates in pre-invasion and post-invasion period in Suisun and delta regions of the upper San Francisco Estuary. Parameter details are listed for Bayesian estimation of the multivariate autoregressive (MAR) model. 'Expected' directions of the interactions (+ positive, - negative, ? unknown, P0 probably zero, 0 zero with high certainty) were specified in the prior probabilities and prior odds were set to 3. 'Deviations' represent $\Delta\beta_{ij}$ from the eq. 4 and indicate substantial changes in relationships from pre-invasion to post-invasion period. Odds ratio (posterior odds / prior odds) is expressed as 1/G for results that were contrary to expectation (G represents odds ratio for the unanticipated result).

Biotic Interactions & Covariates	**Mean ± SD**	**2.50 – 97.50%**	**Post-odds**	**Expected**	**Odds ratio**
Suisun region pre-invasion					
high-quality phytoplankton on omnivores	0.659 ± 0.400	-0.106 – 1.445	20.1	+	6.7
low-quality phytoplankton on omnivores	0.359 ± 0.254	-0.130 – 0.877	13.3	P0	4.4
predators on omnivores	-0.308 ± 0.184	-0.664 – 0.045	23.5	-	7.8
Potamocorbula on nauplii	-0.221 ± 0.165	-0.545 – 0.116	10.5	-	3.5
X_2* on low quality phytoplankton	-0.519 ± 0.329	-1.159 – 0.150	14.5	?	4.8
Suisun region post-invasion					
omnivores on herbivores	-0.646 ± 0.393	-1.408 – 0.173	17.5	-	5.8
herbivores on omnivores	-0.581 ± 0.324	-1.214 – 0.051	27.9	-	9.3
predators on herbivores	-0.376 ± 0.223	-0.829 – 0.072	20.4	-	6.8
omnivores on nauplii	0.658 ± 0.534	-0.416 – 1.698	8.6	-	1/2.9

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nauplii on omnivores	0.958 ± 0.744	-0.481 – 2.364	8.6	+	2.9
predators on omnivores	-0.270 ± 0.204	-0.664 – 0.145	9.9	-	3.3
omnivores on predators	0.873 ± 0.583	-0.263 – 1.968	13.2	+	4.4
X_2 on herbivores	-0.790 ± 0.223	-1.234 – -0.379	Inf.	?	Inf.
X_2 on omnivores	-0.737 ± 0.216	-1.158 – -0.296	799.0	?	266.3
Suisun region deviations					
omnivores on herbivores	-0.856 ± 0.458	-1.720 – 0.074	26.6	-	8.9
herbivores on omnivores	-0.873 ± 0.495	-1.811 – 0.129	21.2	-	7.1
predators on herbivores	-0.417 ± 0.264	-0.947 – 0.104	17.3	-	5.8
nauplii on omnivores	0.947 ± 0.720	-0.492 – 2.343	9.8	+	3.3
Potamocorbula on nauplii	0.430 ± 0.305	-0.176 – 1.033	11.6	-	1/3.9
X_2 on herbivores	-0.510 ± 0.314	-1.160 – 0.079	22.3	?	7.4
X_2 on omnivores	-0.588 ± 0.317	-1.211 – 0.046	27.6	?	9.2
Delta region pre-invasion					
predators on herbivores	-0.477 ± 0.331	-1.156 – 0.171	12.5	-	4.2
small predators on nauplii	-0.810 ± 0.347	-1.477 – -0.110	67.6	-	22.5
omnivores on small predators	-0.506 ± 0.379	-1.276 – 0.255	10.5	P0	3.5
X_2 on nauplii	0.503 ± 0.239	0.026 – 0.979	53.6	?	17.9
Delta region post-invasion					
omnivores on herbivores	-0.512 ± 0.396	-1.295 – 0.297	9.2	-	3.1
X_2 on predators	0.402 ± 0.203	-0.009 – 0.804	34.8	?	11.6
Delta region deviations					
small predators on nauplii	0.819 ± 0.441	-0.043 – 1.690	29.0	-	1/9.7
X_2 on nauplii	-0.442 ± 0.303	-1.052 – 0.136	13.3	?	4.4
X_2 on predators	0.401 ± 0.306	-0.215 – 1.009	10.1	?	3.4

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FIGURES

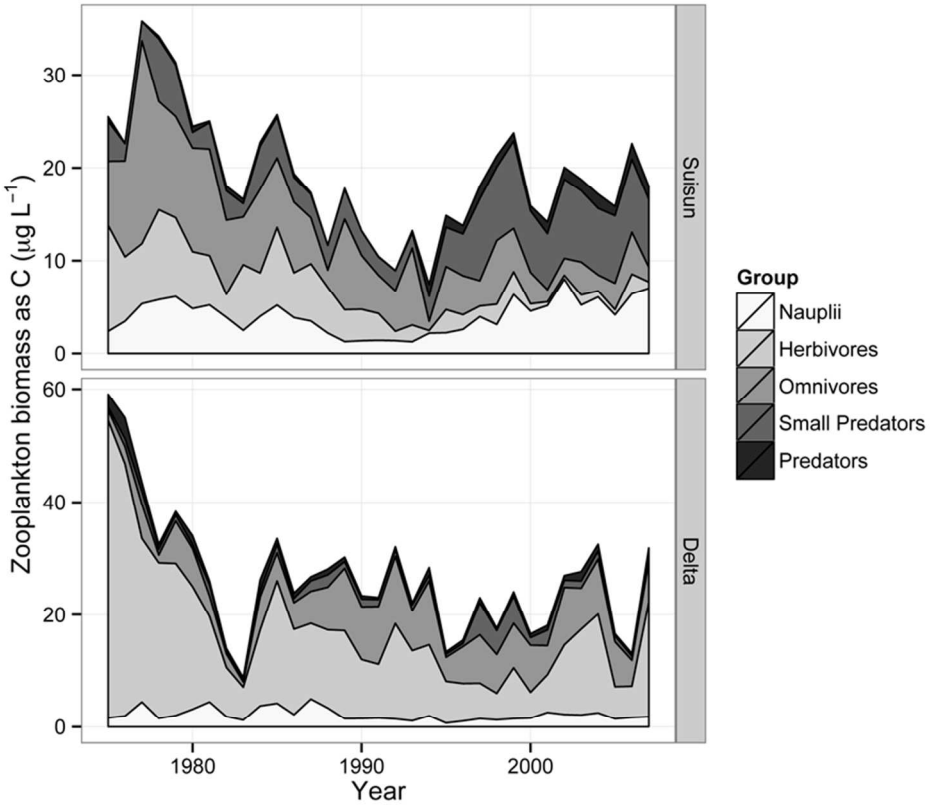

Figure 1. Temporal dynamics of zooplankton annual mean biomass, expressed as µg carbon per L, in two regions of the upper San Francisco Estuary. Zooplankton community in Suisun experienced continuous declines in herbivore (slope of the long-term trend estimated by Mann-Kendall test $b = -6.83\%$ year^{-1}, n = 33, $P < 0.001$) and omnivore ($b = -4.68\%$ year^{-1}, n = 33, $P < 0.001$) biomass. Biomass of predators ($b = 6.13\%$ year^{-1}, n = 33, $P < 0.001$) and small predators ($b = 3.71\%$ year^{-1}, n = 33, $P = 0.001$) in Suisun increased. Zooplankton community in delta experienced continuous declines in herbivore ($b = -3.82\%$ year^{-1}, n = 33, $P < 0.001$) and increased in omnivore ($b = 2.30\%$ year^{-1}, n = 33, $P = 0.008$) biomass.

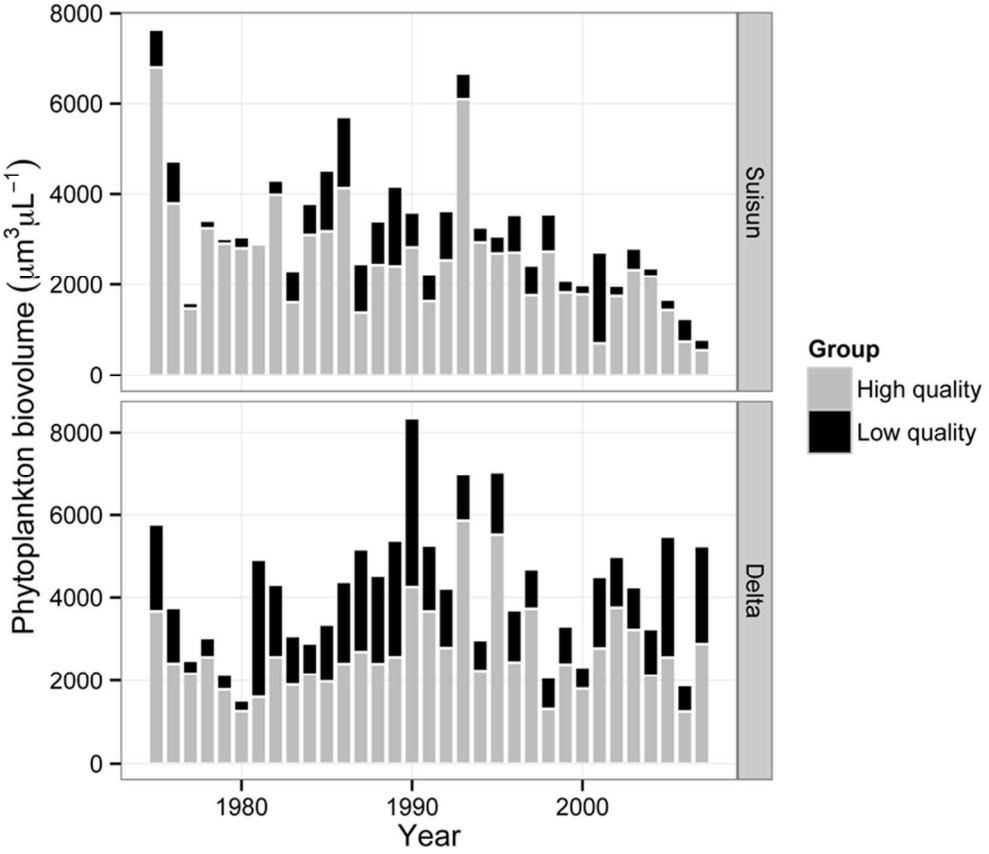

Figure 2. Temporal dynamics of phytoplankton expressed as mean annual biovolume in two regions of the upper San Francisco Estuary. High quality phytoplankton are cryptomonads and diatoms (black bars), low quality phytoplankton (grey bars) encompass all other taxa including cyanobacteria, dinoflagellates, green algae, chrysophytes, euglenoids, synurophytes and haptophytes. High quality phytoplankton (b = –2.50% year^{-1}, n = 33, $P < 0.001$, Mann-Kendall test) and total phytoplankton biovolume (b = –2.37% year^{-1}, n = 33, $P < 0.001$) in Suisun showed declining trends over the study period.

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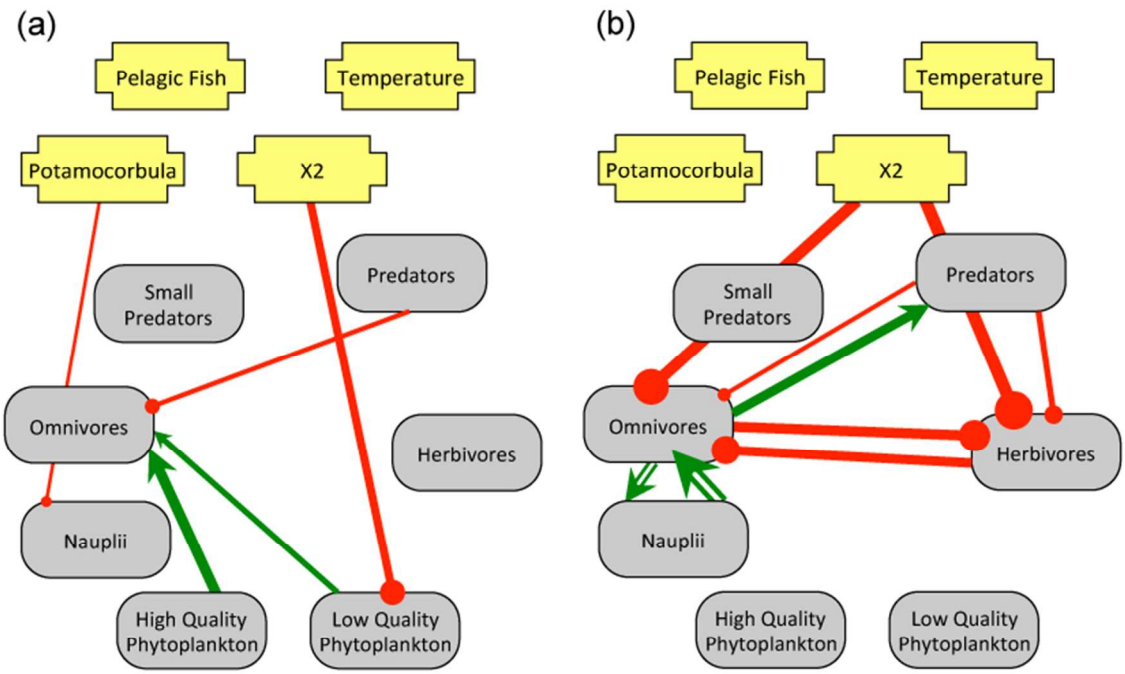

Figure 3. Biotic interactions among plankton functional groups (grey ovals) and influence of major covariates (yellow boxes) in low-salinity Suisun region before (a) and after (b) invasion of several zooplankton species in 1993. Green arrows pointing toward a plankton group indicate positive interactions; red lines indicate negative interactions. The strength of the interactions is represented by the widths of the lines. Only the relationships with substantial support from the data are depicted (OR ≥ 3.2). Two open lines represent interactions that have marginal support from the data (OR = 2.9) but do not meet the criterion for substantial evidence.

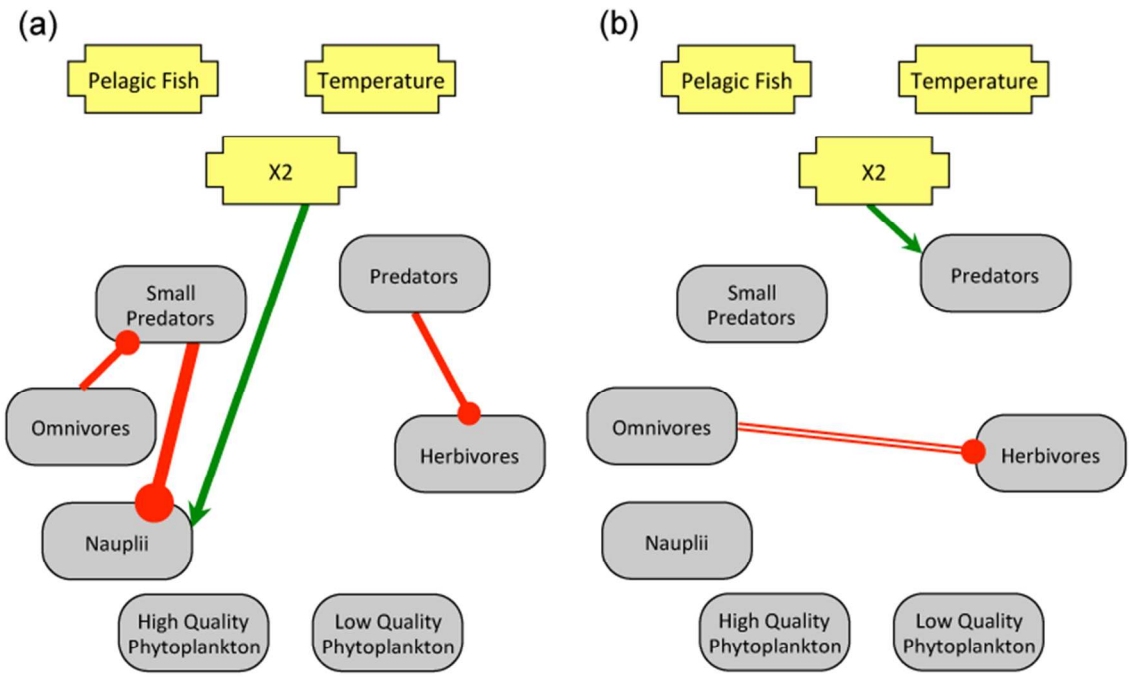

Figure 4. Biotic interactions among plankton functional groups (grey ovals) and influence of major covariates (yellow boxes) in mostly freshwater delta region before (a) and after (b) invasion of several zooplankton species in 1993. Green arrows pointing toward a plankton group indicate positive interactions; red lines indicate negative interactions. The strength of the interactions is represented by the widths of the lines. Only the relationships with substantial support from the data are depicted (OR ≥ 3.2). The open line represents an interaction that has marginal support from the data (OR = 3.1) but does not meet the criterion for substantial evidence.

SUPPORTING INFORMATION

Human-induced biotic invasions and changes in plankton interaction networks

Pavel Kratina, Ralph Mac Nally, Wim J. Kimmerer, James R. Thomson, Monika Winder

Appendix S1. Supporting methods.

Formulation of the multivariate autoregressive model (MAR)

We represented dynamics of the seven plankton groups ('focal groups') with the Gompertz model (Dennis *et al.* 2006), beginning with a deterministic version (Reddingius 1971):

$$n_{i,t} = n_{i,t-1}\exp\left(\gamma_i + \delta_i \ln\left(n_{i,t-1}\right)\right). \quad (1)$$

Here, $n_{i,t}$ is the biomass of functional group *i* at time *t*, $n_{i,t-1}$ is the biomass of group *i* at the previous time step, γ_i is the intrinsic rate of population growth for group *i*, and δ_i, which has been interpreted as the degree of density dependence. By taking natural logarithms and by setting $x_{i,t} = \ln(n_{i,t})$, (1) becomes:

$$x_{i,t} = x_{i,t-1} + \gamma_i + \delta_i x_{i,t-1}. \quad (2)$$

Interspecific interactions among the *J* plankton groups were incorporated by appending terms relating to the previous year $\beta_{ij}x_{j,t-1}$, excluding intra-group terms:

$$x_{i,t} = x_{i,t-1} + \gamma_i + \delta_i x_{i,t-1} + \sum_{j=1,j\neq i}^{J} \beta_{ij} x_{j,t-1}. \quad (3a)$$

The interaction terms among the plankton functional groups were implemented as potentially differing between the pre- and post-invasion periods by using an indicator variable *I*, which was 0 for the pre-invasion period and unity afterwards:

$$x_{i,t} = x_{i,t-1} + \gamma_i + \delta_i x_{i,t-1} + \sum_{j=1,j\neq i}^{J} \left(\beta_{ij}^{0} + I_t \Delta\beta_{ij}\right) x_{j,t-1}. \quad (3b)$$

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Here, the pre-invasion values are β_{ij}^{0} and the post-invasion values are $\left(\beta_{ij}^{0} + I_t \Delta\beta_{ij}\right)$. Changes in the relationships from the pre-invasion to the post-invasion period (i.e., deviations) are $\Delta\beta_{ij}$. We included the effects of the *K* covariates u_k through α-coefficients, for the current year *t,* which were also allowed to differ after the invasions:

$$x_{i,t} = x_{i,t-1} + \gamma_i + \delta_i x_{i,t-1} + \sum_{j=1,j\neq i}^{J}\left(\beta_{ij}^{0} + I_t \Delta\beta_{ij}\right)x_{j,t-1} + \sum_{k=1}^{K}(\alpha_{ik}^{0} + I_t \Delta\alpha_{ik})u_{k,t}. \quad (4)$$

Bayesian estimation of the MAR model

We used Bayesian methods to estimate the model because measurement uncertainties can be incorporated using hierarchical models and sporadically distributed missing data are handled easily within the same process by which the parameter estimates are made. Equation (4) was estimated by using the following model in WinBUGS, v. 1.4 (Spiegelhalter, Thomas & Best 2003):

$$z_{i,t} \sim N\left(x_{i,t}, \omega_{i,t}^{2}\right); x_{i,t} \sim N\left(\mu_{i,t}, \sigma_i^{2}\right); \acute{c}_{k,t} \sim N\left(u_{k,t}, \zeta_{k,t}^{2}\right); \quad (5a)$$

$$\mu_{i,t} = x_{i,t-1} + \gamma_i + \delta_i x_{i,t-1} + \sum_{j=1,j\neq i}^{J}\left(\beta_{ij}^{0} + I_t \Delta\beta_{ij}\right)x_{j,t-1} + \sum_{k=1}^{K}(\alpha_{ik}^{0} + I_t \Delta\alpha_{ik})u_{k,t}. \quad (5b)$$

Here, *N* denotes the normal distribution. The model states that the (ln-transformed) observed values ($z_{i,t}$) represent the true values ($x_{i,t}$), which have observation errors. These were included by the use of (ln-transformed) unobserved values ($x_{i,t}$) and observation errors, $\omega_{i,t}^{2}$. The observation errors were estimated from standard errors (SEs) of mean values for the response variables for each time period. The $z_{i,t}$ were ln-transformed, so we used the first term of a Taylor functional expansion to approximate the ln-transformed SEs $[SE(\ln(\bar{n})) \approx SE(\bar{n})/\bar{n}]$ (Seber 1973; Stuart & Ord 1987).

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Process variances (σ_i^2) were group-specific and were implemented with uninformative priors on σ_i of $U(0.01, 10)$ (Gelman 2005), where U denotes a uniform distribution. The true, unobserved values ($\mu_{i,t}$) are functions of the groups-dynamic parameters, biotic interactions, and covariates (eq. 4).

The observed covariates $c_{k,t}$ were standardized [$\acute{c}_{k,t} = (c_{k,t} - \bar{c}_k)/SD_k$] in order to aid model convergence and to equalize numerical ranges among different scales of measurement. Uncertainties in covariate measurements (within-year SEs) were scaled by the inter-annual standard deviations (i.e., $SE_{k,t}/SD_k$). The model specifies that the true (standardized) covariate values ($u_{k,t}$) are related to the observed standardized values ($\acute{c}_{k,t}$) but include the covariate-specific uncertainties [$\zeta_{k,t}^2 = (SE_{k,t}/SD_k)^2$].

Prior probabilities and parameter inference

For the important ecological parameters, α^0 and β^0, we used both informative (offset normal) and uninformative (standard normal) priors. The offsets were $N(0.675,1)$ and $N(-0.675,1)$ for expected positive and negative relationships; these values invest a c. 3:1 prior probability mass in favor of the expected influence. While there are plausible intraspecific density-dependencies in plankton dynamics over short periods of time (e.g., phytoplankton spring bloom), here we assumed no interannual intraspecific density dependence within the plankton groups: $\delta_i \sim N(0, 10^{-3})$. Several of the possible relationships were specifically excluded from the model (i.e., deemed unlikely to be important). For such relationships, coefficients were assigned $N(0, 10^{-6})$ priors (i.e., 0 with high certainty). For change parameters, $\Delta\alpha$ and $\Delta\beta$, we used

standard normal prior distributions $N(0,1)$, except for those involving implausible relationships, which were fixed at zero.

Model convergence and adequacy

The model was estimated with three MCMC chains of 20 000 iterations after 10 000 iterations of burn-in ('model settling'), results for which were discarded. We checked for MCMC mixing and convergence using the boa package (Smith 2006) in *R* (R Development Core Team 2013). We determined the adequacy of model fit by using posterior predictive assessment (Gelman, Meng & Stern 1996). This involves simulating samples from the $(\mu_{i,t}, \sigma_i^2)$, $\eta_{i,t}$. An adequate measure of fit for an observation for a normal variate is $|x_{i,t} - \mu_{i,t}|$ for the data and $|\eta_{i,t} - \mu_{i,t}|$ for the simulated values respectively (Agresti 2002). These values are summed over all (i,t) combinations. A good model fit has the observed summed value in the middle of the distribution of simulated summed discrepancies, so a posterior predictive probability (*PPP*) of 0.5 indicates a perfect fit, whereas *PPP* values close to zero or unity indicate poor fit. Our results demonstrated that posterior predictive assessment was 0.14 for Suisun and 0.18 for the delta, suggesting that the data plausibly could be generated from the parameters and structure of the models.

We determined the relative importance of the autoregressive (A), among-focal group (F), and covariate (C) components in the model. We calculated the R^2 for eight models: null (fitting constant-only averages for the focal group variables), A, F, C, A + F, A + C, F + C, A + F + C (full model). Values of R^2 for these models were estimated by omitting terms from eq. (5) as appropriate. The γ_i terms were retained for all models. R^2

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were the squared Pearson correlation coefficients between the *z* and □ values from the focal group values for all years. We performed hierarchical partitioning to decompose variance (Chevan & Sutherland 1991; Mac Nally 2000), which identifies independent contributions from individual terms (viz., A, F, and C) and joint variance explained; the R package hier.part (Walsh & Mac Nally 2003) was used for this task.

Supporting References

Agresti, A. (2002) *Categorical data analysis*. Wiley, New York.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *The American Statistician,* **45,** 90-96.

Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L. & Staples, D.F. (2006) Estimating density dependence, process noise, and observation error. *Ecological Monographs,* **76,** 323-341.

Gelman, A. (2005) Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis,* **1,** 1-19.

Gelman, A., Meng, X.-L. & Stern, H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica,* **6,** 733-787.

Mac Nally, R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—'predictive' and 'explanatory' models. *Biodiversity and Conservation,* **9,** 655-671.

For Peer Review

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.

Reddingius, J. (1971) Gambling for existence: a discussion of some theoretical problems in animal population ecology. *Acta Biotheoretica,* **20 (supp.),** 1-208.

Seber, G.A.F. (1973) *The estimation of animal abundance and related parameters*. Griffin, London.

Smith, B. (2006) Bayesian Output Analysis Program (BOA) for MCMC.

Spiegelhalter, D., Thomas, A. & Best, N. (2003) WinBUGS version 1.4. Bayesian inference using Gibbs sampling. MRC Biostatistics Unit, Institute for Public Health, Cambridge, UK.

Stuart, A. & Ord, J.K. (1987) *Kendall's advanced theory of statistics*. Oxford University Press, New York.

Walsh, C. & Mac Nally, R. (2003) The hier.part package. Hierarchical Partitioning. R project for statistical computing. URL: http://cran.r-project.org/.

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