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1 **Human-induced biotic invasions and changes in plankton interaction networks**

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21

22 SUMMARY

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

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

50

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

53

54 INTRODUCTION

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

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

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

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

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

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

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

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

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127 MATERIALS AND METHODS

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

140 **Response variables and covariates**

141 *Zooplankton biomass*

142 Zooplankton samples were collected using oblique tow nets (154 μm mesh size) or pumped
143 through a 64 μm mesh, bi-weekly or monthly (for details of the methods see Orsi & Mecum
144 1986). We converted zooplankton densities to carbon biomass and calculated annual means
145 (Winder & Jassby 2011) to capture shifts in the long-term biomass of key functional groups (Fig.
146 1). We used time-series data from six consistently sampled locations in Suisun and from seven
147 consistently sampled locations in the delta.

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

150 stages of copepods and are also an important food for omnivorous and predatory zooplankton,
151 clams, and larval fish. Herbivores are suspension feeders consuming phytoplankton. They can
152 compete with, or serve as food for, other zooplankton groups. Herbivores include native
153 cladocerans, such as *Daphnia* spp., *Bosmina* spp., *Diaphanosoma* spp., and rotifers such as
154 *Asplanchna* spp., *Keratella* spp., *Polyarthra* spp., *Synchaeta* spp. and *Trichocerca* spp.
155 Omnivores feed on phytoplankton, suspended particulate matter, and smaller zooplankton
156 including their juvenile stages; omnivores include three probably native species of *Acartia* spp.,
157 *Eurytemora affinis*, and introduced *Pseudodiaptomus* spp., and *Sinocalanus doerrii*. We
158 characterize the group ‘small predators’ as zooplankton of smaller sizes (< 500 µm) that likely
159 derive carbon from the microbial pool, feeding on ciliates, flagellates, and some taxa also on
160 detritus and bacteria. This group is composed largely of introduced cyclopoids *Limnoithona* spp.,
161 and *Oithona davisae*, and harpacticoids. The ‘predators’ include native *Acanthocyclops* spp. and
162 introduced *Acartiella sinensis* and *Tortanus dextrilobatus* which can reach ten times the
163 individual body mass of the ‘small predators’ (Gould & Kimmerer 2010). This group is at the top
164 of the planktonic food web, largely feeding on other zooplankton species (Hooff & Bollens
165 2004; York *et al.* 2013).

166

167 *Phytoplankton biovolume*

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

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

179

180 *Biotic and abiotic covariates*

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

196 and D7-C) that were sampled the same sampling period. Two abiotic covariates were annual
197 means of surface temperature, recorded at the same locations and time as the zooplankton
198 samples were collected, and the distance from the mouth of the estuary of the daily-averaged,
199 near-bottom salinity of 2 (practical salinity scale), locally termed 'X₂' (Jassby *et al.* 1995). X₂ is
200 a synthetic measure of the physical responses of the estuary to freshwater flow (Monismith *et al.*
201 2002).

202

203 **Statistical methods**

204 We used a variant of a multivariate, autoregressive model (MAR; Ives *et al.* 2003; Supporting
205 Information) to analyze the dynamics of plankton functional groups. The MAR method was
206 developed to estimate ecological interactions from time-series data and has been applied to
207 plankton interaction networks in freshwater (e.g., Ives *et al.* 2003; Hampton, Scheuerell &
208 Schindler 2006) and marine (e.g., Francis *et al.* 2012) ecosystems. We built separate MAR
209 models for each region, which included time-dependent parameters that tested for differences in
210 intra-specific interactions and covariate effects between the pre- (1974-1992) and post- (1993-
211 2008) invasions periods. The Bayesian framework allowed us to incorporate our prior
212 expectations for the direction of biotic interactions and the effects of main covariates. We used
213 normal prior distributions with unit variance and means that reflected prior expectations for the
214 direction of influence, i.e. $N(\mu, 1)$, with $\mu = -0.675, +0.675$ and 0 for parameters with negative,
215 positive, or unknown prior expectations, respectively (Mac Nally *et al.* 2010). Parameters
216 quantifying changes in intra-specific interactions or covariate effects were assigned
217 uninformative, standard normal prior distributions, $N(0,1)$. The informative normal priors
218 corresponded to prior odds of 3:1 in favour of the expected direction of influence (Mac Nally *et*

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

228

229 **RESULTS**

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

237

238 *Relationships in the Suisun region*

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

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

258
259 *Relationships in the delta region*

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

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

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

275 **DISCUSSION**

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

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

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

304 We expected to detect competitive effects of *L. tetraspina* on other groups because after
305 1993 this small predator became the numerically dominant in Suisun. However, ‘small predators’
306 appeared to have little association with other plankton groups. *L. tetraspina* feeds preferentially
307 on protists, but rarely consumes diatoms (Bouley & Kimmerer 2006) and it is too small to
308 consume calanoid copepods. Our results are consistent with laboratory experiments (Bouley &
309 Kimmerer 2006) and suggest that *L. tetraspina* may not compete with or prey upon native
310 zooplankton groups. The negative effect of small predators on nauplii in the delta declined after
311 the establishment of *L. tetraspina* in 1993 in an agreement with this species being a source rather
312 than a consumer of nauplii. Nevertheless, *Limnoithona* spp. may be a resource for predatory
313 zooplankton (York *et al.* 2013). The weakening of the negative correlation between predators
314 and herbivores after 1993 in the delta region is consistent with a shift from the native predators
315 *Acanthocyclops* spp. to invasive *A. sinensis*.

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

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

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

335 Prior studies have documented a negative effect of *Potamocorbula* on phytoplankton,
336 copepod nauplii, and individual species of zooplankton and fish (Alpine & Cloern 1992;
337 Kimmerer, Gartside & Orsi 1994; Kimmerer 2006). Our study suggests a negative effect of
338 *Potamocorbula* on nauplii in Suisun before 1993, where relatively high nauplius biomass sharply
339 declined soon after the introduction of *Potamocorbula* in 1986 (see also Kimmerer, Gartside &
340 Orsi 1994). Nauplii did not appear to be negatively affected by the clam after 1993, but increased
341 due to the recruitment of new invasive zooplankton, mainly *Limnoithona* spp. (Winder & Jassby
342 2011). The lack of response of plankton to *Potamocorbula* abundance in our study may relate to

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

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

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

360 We used time-series data aggregated annually and across large geographical areas (about
361 1000 km²) to remove the effect of seasonal events (e.g., Micheli 1999) and to focus our analysis
362 on long-term trends of plankton dynamics across the regions. Therefore, some short-term or
363 locally important interactions may not have been detected. The MAR analysis assumes linear
364 relationships (on the log-scale), so any non-linear relationships may not have been revealed (Ives
365 *et al.* 2003). Despite these limitations, our results suggested several relationships, some

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

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

381 There are few studies that investigate changes in the biotic network structure following
382 invasions of non-native species. Recent exceptions that focused on the complex plant–pollinator
383 networks in terrestrial systems found no effect of invasive species on overall connectance (the
384 number of realized links relative to the number of possible links; Aizen, Morales & Morales
385 2008; Heleno *et al.* 2009), but the connectance among native species declined (Aizen, Morales &
386 Morales 2008). Our analysis of a simplified network among plankton functional groups suggests
387 that connectance can either increase (Suisun) or decline (Δ), following the invasions (Figs 3,

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

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

398

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551

552

553 **SUPPORTING INFORMATION**

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

555 **Appendix S1.** Supporting methods.

556

For Peer Review

557 **Table 1.** Statistical comparison of major biotic interactions and covariates in pre-invasion and
 558 post-invasion period in Suisun and delta regions of the upper San Francisco Estuary. Parameter
 559 details are listed for Bayesian estimation of the multivariate autoregressive (MAR) model.
 560 ‘Expected’ directions of the interactions (+ positive, - negative, ? unknown, P0 probably zero, 0
 561 zero with high certainty) were specified in the prior probabilities and prior odds were set to 3.
 562 ‘Deviations’ represent $\Delta\beta_{ij}$ from the eq. 4 and indicate substantial changes in relationships from
 563 pre-invasion to post-invasion period. Odds ratio (posterior odds / prior odds) is expressed as 1/G
 564 for results that were contrary to expectation (G represents odds ratio for the unanticipated result).
 565

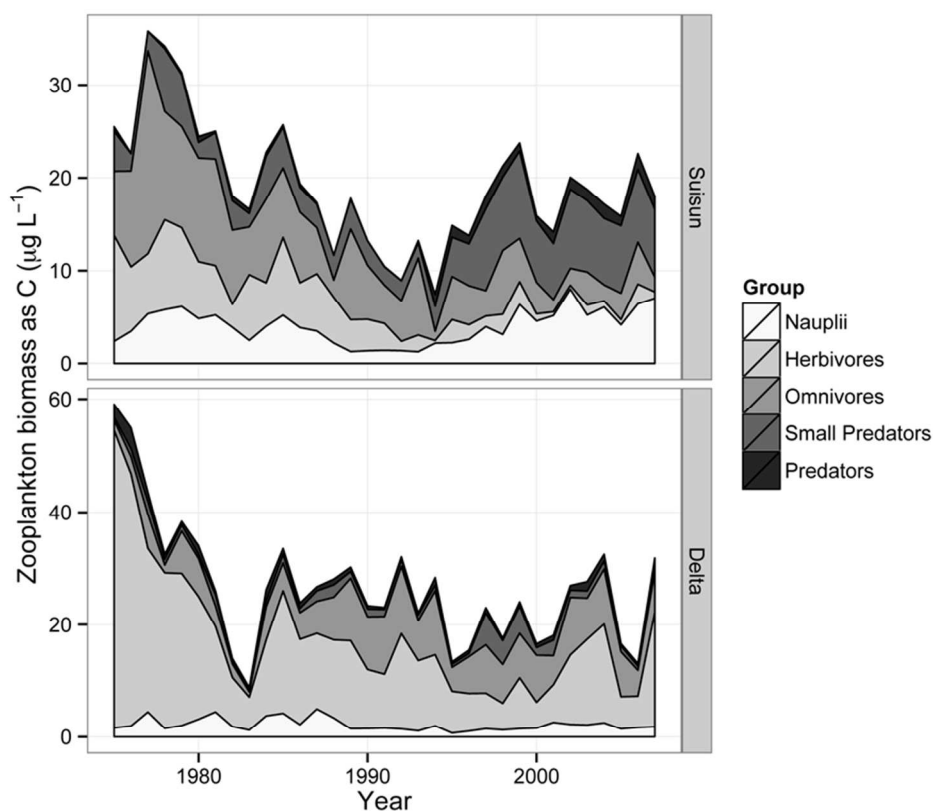
Biotic Interactions & Covariates	Mean \pm SD	2.50 – 97.50%	Post-odds	Expected	Odds ratio
Suisun region pre-invasion					
high-quality phytoplankton on omnivores	0.659 \pm 0.400	-0.106 – 1.445	20.1	+	6.7
low-quality phytoplankton on omnivores	0.359 \pm 0.254	-0.130 – 0.877	13.3	P0	4.4
predators on omnivores	-0.308 \pm 0.184	-0.664 – 0.045	23.5	-	7.8
<i>Potamocorbula</i> on nauplii	-0.221 \pm 0.165	-0.545 – 0.116	10.5	-	3.5
X ₂ * on low quality phytoplankton	-0.519 \pm 0.329	-1.159 – 0.150	14.5	?	4.8
Suisun region post-invasion					
omnivores on herbivores	-0.646 \pm 0.393	-1.408 – 0.173	17.5	-	5.8
herbivores on omnivores	-0.581 \pm 0.324	-1.214 – 0.051	27.9	-	9.3
predators on herbivores	-0.376 \pm 0.223	-0.829 – 0.072	20.4	-	6.8
omnivores on nauplii	0.658 \pm 0.534	-0.416 – 1.698	8.6	-	1/2.9

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
<i>Potamocorbula</i> 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

566

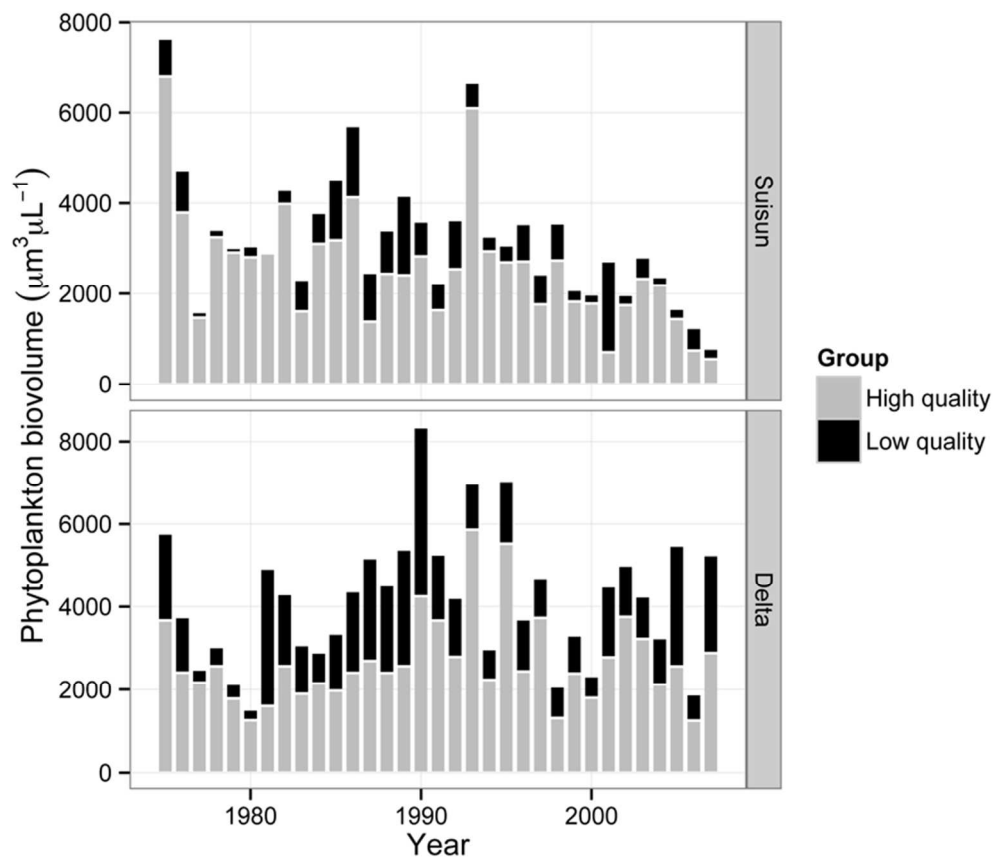
567

568 FIGURES



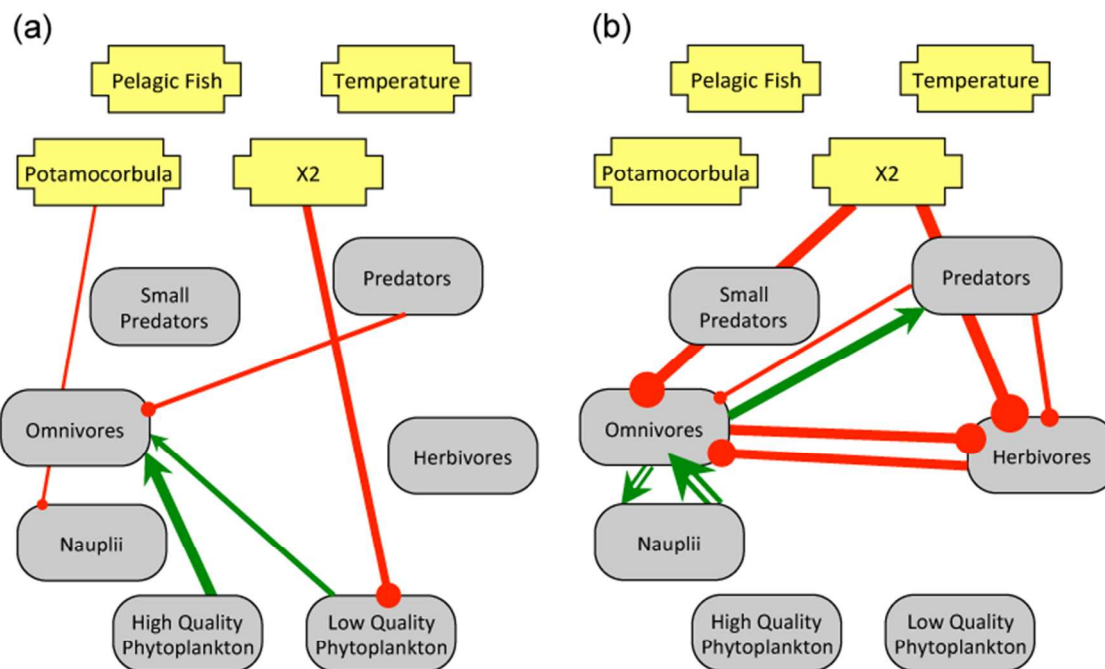
569

570 **Figure 1.** Temporal dynamics of zooplankton annual mean biomass, expressed as µg carbon per
 571 L, in two regions of the upper San Francisco Estuary. Zooplankton community in Suisun
 572 experienced continuous declines in herbivore (slope of the long-term trend estimated by Mann-
 573 Kendall test $b = -6.83\% \text{ year}^{-1}$, $n = 33$, $P < 0.001$) and omnivore ($b = -4.68\% \text{ year}^{-1}$, $n = 33$, $P <$
 574 0.001) biomass. Biomass of predators ($b = 6.13\% \text{ year}^{-1}$, $n = 33$, $P < 0.001$) and small predators
 575 ($b = 3.71\% \text{ year}^{-1}$, $n = 33$, $P = 0.001$) in Suisun increased. Zooplankton community in delta
 576 experienced continuous declines in herbivore ($b = -3.82\% \text{ year}^{-1}$, $n = 33$, $P < 0.001$) and
 577 increased in omnivore ($b = 2.30\% \text{ year}^{-1}$, $n = 33$, $P = 0.008$) biomass.

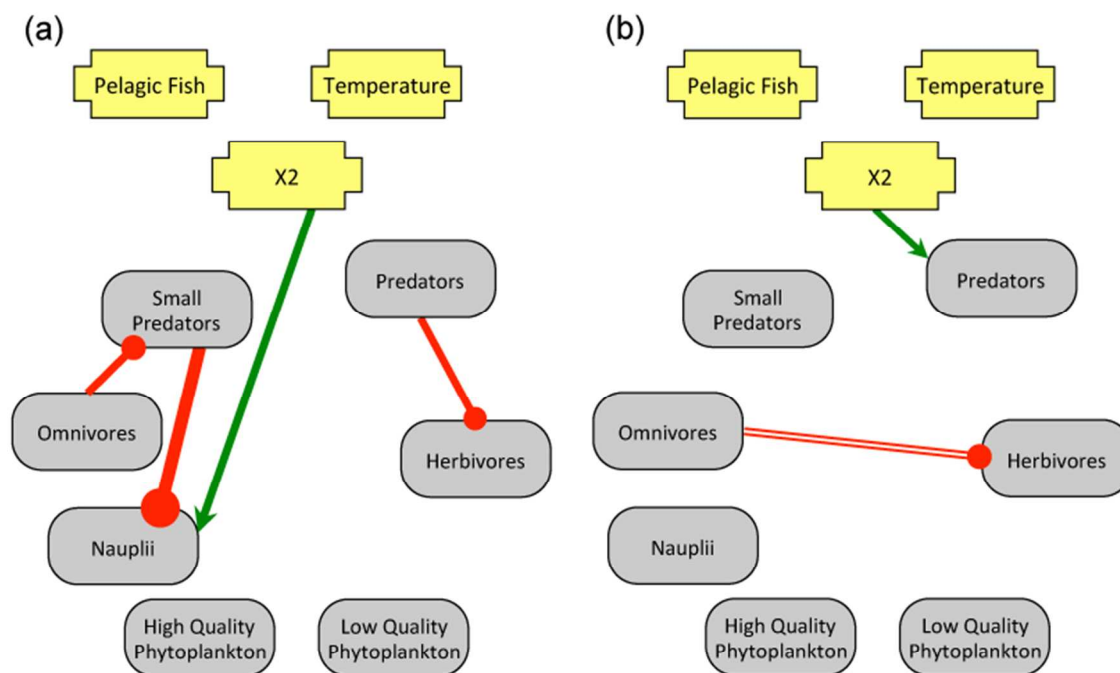


578

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



586
 587 **Figure 3.** Biotic interactions among plankton functional groups (grey ovals) and influence of
 588 major covariates (yellow boxes) in low-salinity Suisun region before (a) and after (b) invasion of
 589 several zooplankton species in 1993. Green arrows pointing toward a plankton group indicate
 590 positive interactions; red lines indicate negative interactions. The strength of the interactions is
 591 represented by the widths of the lines. Only the relationships with substantial support from the
 592 data are depicted ($OR \geq 3.2$). Two open lines represent interactions that have marginal support
 593 from the data ($OR = 2.9$) but do not meet the criterion for substantial evidence.



594

595 **Figure 4.** Biotic interactions among plankton functional groups (grey ovals) and influence of
 596 major covariates (yellow boxes) in mostly freshwater delta region before (a) and after (b)
 597 invasion of several zooplankton species in 1993. Green arrows pointing toward a plankton group
 598 indicate positive interactions; red lines indicate negative interactions. The strength of the
 599 interactions is represented by the widths of the lines. Only the relationships with substantial
 600 support from the data are depicted ($OR \geq 3.2$). The open line represents an interaction that has
 601 marginal support from the data ($OR = 3.1$) but does not meet the criterion for substantial
 602 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):

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

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:

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

Here, the pre-invasion values are β_{ij}^0 and the post-invasion values are $(\beta_{ij}^0 + I_t \Delta \beta_{ij})$.

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:

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

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):

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

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

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).

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 [$\hat{c}_{k,t} = (c_{k,t} - \bar{c}_k)/SD_k$] 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 ($\hat{c}_{k,t}$) 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

were the squared Pearson correlation coefficients between the z and \square 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.

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