

Bottom-up linkages between primary production, zooplankton, and fish in a shallow, hypereutrophic lake

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Abstract. Nutrient supply is a key bottom-up control of phytoplankton primary production in lake ecosystems. Top-down control via grazing pressure by zooplankton also constrains primary production and primary production may simultaneously affect zooplankton. Few studies have addressed these bidirectional interactions. We used convergent cross-mapping (CCM), a numerical test of causal associations, to quantify the presence and direction of the causal relationships among environmental variables (light availability, surface water temperature, NO₃-N, and PO₄-P), phytoplankton community composition, primary production, and the abundances of five functional zooplankton groups (large cladocerans, small cladocerans, rotifers, calanoids, and cyclopoids) in Lake Kasumigaura, a shallow, hypereutrophic lake in Japan. CCM suggested that primary production was causally influenced by NO₃-N and phytoplankton community composition; there was no detectable evidence of a causal effect of zooplankton on primary production. Our results also suggest that rotifers and cyclopoids were forced by primary production, and cyclopoids were further influenced by rotifers. However, our CCM suggested that primary production was weakly influenced by rotifers (i.e., bidirectional interaction). These findings may suggest complex linkages between nutrients, primary production, and rotifers and cyclopoids, a pattern that has not been previously detected or has been neglected. We used linear regression analysis to examine the relationships between the zooplankton community and pond smelt (*Hypomesus nipponensis*), the most abundant planktivore and the most important commercial fish species in Lake Kasumigaura. The relative abundance of pond smelt was significantly and positively correlated with the abundances of rotifers and cyclopoids, which were causally influenced by primary production. This finding suggests that bottom-up linkages between nutrient, primary production, and zooplankton abundance might be a key mechanism supporting high planktivore abundance in eutrophic lakes. Because increases in primary production and cyanobacteria blooms are likely to occur simultaneously in hypereutrophic lakes, our study highlights the need for ecosystem management to resolve the conflict between good water quality and high fishery production.

Key words: convergent cross-mapping (CCM); causal network; ecosystem functioning; energy transfer efficiency; inland fisheries; long-term monitoring; microzooplankton; nutrient limitation; nutrient loading; photosynthesis; trophic cascade; water quality.

INTRODUCTION

Phytoplankton primary production, the storage of energy through the formation of organic matter from inorganic carbon compounds, is a cornerstone of ecosystem processes and a key supporting ecosystem service in aquatic ecosystems (Karlsson et al. 2009, Cardinale et al. 2012, Pace and Lovett 2013). The organic matter supplied by primary production is necessary for the maintenance of higher trophic levels, such as zooplankton and fish, but in lake ecosystems, excessive primary production as a consequence of nutrient loading can cause undesirable algal blooms, bottom-water hypoxia, and loss of biodiversity (Downing et al. 1990, Cole 2009, Bunnell et al. 2014). Elucidating the factors and mechanisms that determine primary production and understanding how primary production links to higher trophic level organisms are therefore essential for management of both water quality and fisheries.

Both bottom-up and top-down forces determine primary production, although the relative importance of these forces can vary greatly among systems and conditions (Pace et al. 1999, Carpenter et al. 2001). Phosphorus and nitrogen loadings are the principal drivers that determine variations in phytoplankton biomass and primary production (Schindler 1977, Elser et al. 2009). Light availability, which is altered by the resuspension of sediment and by variations of dissolved organic carbon concentrations, is a bottom-up force that can influence primary production (Karlsson et al. 2009, Pilati et al. 2009). In contrast to these bottom-up forces, trophic cascades originating from piscivorous and planktivorous fishes can affect primary production via grazing pressures (Carpenter and Kitchell 1988, Schindler et al. 1997). Planktivores, for example, can largely eliminate large-bodied zooplankton such as *Daphnia* species and thereby reduce grazing and increase primary production. Food web structure can substantially change primary production, even if the level of nutrient loading is the same (Carpenter et al. 2001).

Whereas zooplankton control primary production via grazing, some studies have demonstrated a positive correlation between primary production and the abundance or biomass of zooplankton (Pace 1986, Pace et al. 1998,

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Carpenter et al. 2001, Yoshida et al. 2003). The addition of nutrients to lakes increases primary production, some of which is consumed by zooplankton. The positive effects of primary production on zooplankton may thus override the negative impacts of grazing on primary production (Carpenter et al. 1998, Pilati et al. 2009). Similar to the strong bottom-up linkages have been reported between environmental factors, phytoplankton, zooplankton, and fish in marine ecosystems (Richardson and Schoeman 2004, Ware and Thomson 2005), Bunnell et al. (2014) have reported that a reduction of nutrient loadings in eutrophic lakes causes considerable declines in primary productivity and the abundances of zooplankton and fish. Hence, primary production and zooplankton are bidirectionally coupled, and the magnitudes of the couplings may differ between ecosystems and even among different species or functional group in the same ecosystem. However, there is limited evidence to elucidate these bidirectional interactions.

Long-term ecological data sets provide opportunities for identifying the causal networks and determining the strength of species interactions and drivers of community dynamics. This information is critically important for understanding how a system is changed or maintained and for recommending effective management strategies (Hampton et al. 2008, Hughes et al. 2017). In lake systems, analyzing long-term data sets can be useful compared to experiments, because resources and plankton communities change rapidly, and some interactions can be weakly coupled. Time-series statistical tools, such as multivariate auto-regression (MAR) or multivariate autoregressive state space (MARSS) models, have been successfully used to investigate the structural features of plankton communities and the relative importance of top-down and bottom-up drivers in determining phytoplankton biomass or primary production (e.g., Ives et al. 2003, Walsh et al. 2016, Carter et al. 2017). An alternative method, convergent cross-mapping (CCM), a non-linear numerical test of causal associations, has been developed recently to distinguish causality from “mirage correlations,” linear relationships that appear and disappear or even change sign as time goes on (Sugihara et al. 2012). Mirage correlations are known to arise in nonlinear dynamical systems (Deyle et al. 2016a, b, McGowan et al. 2017). In contrast to autoregressive models, CCM is based on an algorithm that compares the ability of lagged components of one process to estimate the dynamics of another and detects causal links by tracking the flow of information through a dynamical system. CCM is capable of detecting bidirectional causality when variables interact with each other in a nonlinear system (Tsonis et al. 2015). That capability can be an advantage for identifying the direction of forcing (top-down and bottom-up).

The goal of this study was to identify the bottom-up and top-down drivers of primary production and to explore the relationships between primary production and zooplankton in Lake Kasumigaura, a shallow, hypereutrophic lake in Japan. We applied CCM to a long-term monitoring data set for Lake Kasumigaura (1996–2015) and quantified the presence and direction of the causal relationships between environmental variables, phytoplankton community composition, primary production, and zooplankton. We considered light availability, water temperature, and dissolved

nutrients as environmental drivers, because these factors have been reported to affect primary production or phytoplankton biomass (Takamura et al. 1987, 1992, Tomioka et al. 2011, Fukushima and Arai 2015). For zooplankton, we used the abundances of five zooplankton functional groups (large cladocerans, small cladocerans, rotifers, cyclopoids, and calanoids; Takamura et al. 2017). We also examined the causal interactions between phytoplankton abundance and other variables to elucidate the difference between phytoplankton abundance and primary production in the context of bottom-up and top-down effects. Moreover, we explored the relationship between zooplankton and pond smelt (*Hypomesus nipponensis*), the most abundant planktivore and the most commercially important species in this lake. For these relationships, we used linear regression instead of CCM, because only the annual catch and fishing effort data on pond smelt were available (i.e., the time series was too short for CCM). We show the possible bottom-up linkages between nutrients, primary production, zooplankton, and planktivores in shallow, eutrophic lakes.

METHODS

Lake Kasumigaura and long-term monitoring data

Lake Kasumigaura, which is located approximately 60 km northeast of Tokyo (Fig. 1), is the second largest lake in Japan, with a surface area of 167.7 km², a total volume of 622 million m³, a mean depth of approximately 4 m, and a maximum depth of 7.4 m. The average water residence time is approximately 200 d. Because of its extremely high loads of organic matter and nutrients, Lake Kasumigaura is well known as a hypereutrophic lake. The fishery of Lake Kasumigaura has played a central role in Japanese inland fisheries. The major commercial fish species are pond smelt, ice fish (*Salangichthys microdon*), freshwater prawn (*Macrobrachium nipponense*) and the gobiid fish (*Tridentiger brevispinis*).

The National Institute for Environmental Studies (NIES) has been conducting monthly monitoring in Lake Kasumigaura since 1976 (Takamura 2012, Takamura and Nakagawa 2016, Takamura et al. 2017). Lake Kasumigaura is registered as a core site of the Japan Long-term Ecological Research Network (JaLTER) and as a trend-monitoring station of the United Nations Global Environment Monitoring System Water Trend Monitoring Project (GEMS/Water). The monitoring data sets are available on the Lake Kasumigaura Database and some data sets have been published in data papers (Takamura and Nakagawa 2016, Takamura et al. 2017; *data available online*).⁴ We used monthly data on light availability (light-extinction coefficient), surface water temperature, primary production, soluble reactive phosphorus (PO₄-P), nitrate nitrogen (NO₃-N), and zooplankton abundance (Appendix S1: Figs. S1, S2) at the center of the lake (Fig. 1, 36°02.142' N, 140°24.222' E, water depth ~5.8 m). Because CCM analysis generally requires taking consecutive time lags of observed variables, we analyzed data from April 1996 to March 2015 (228 months). There were no missing data for any variables during this time interval.

⁴ <http://db.cger.nies.go.jp/gem/moni-e/inter/GEMS/database/kasumi/index.html>

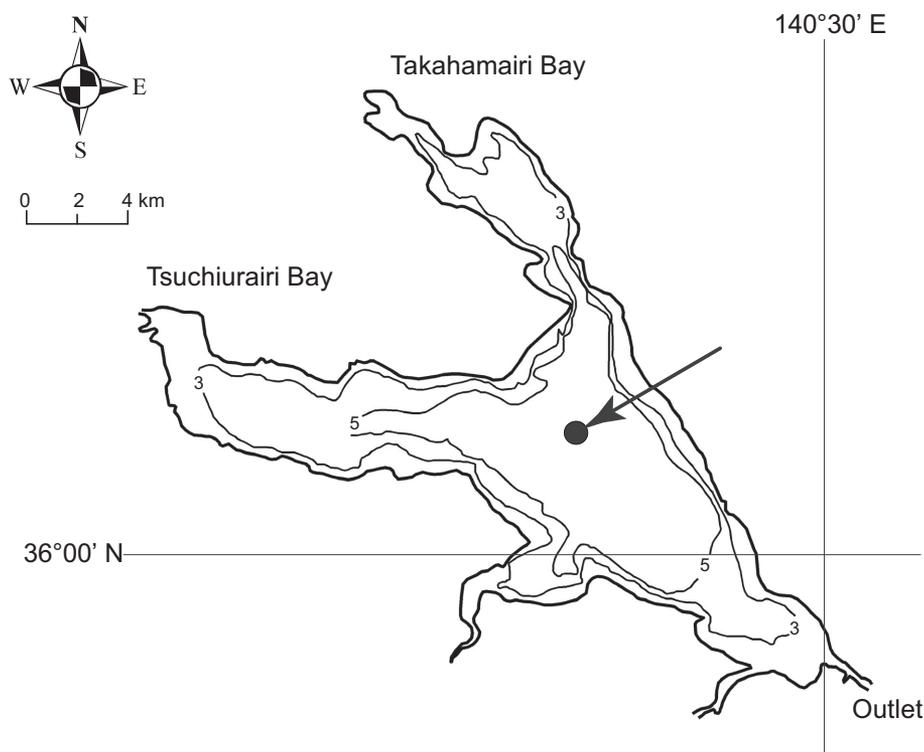


FIG. 1. Map showing the sampling station (lake center) in Lake Kasumigaura, Japan. Depth contours are in meters.

Water temperature was measured at a depth of 0.5 m. Photosynthetically active radiation (PAR) in the water column was measured at every 0.5 m in depth with an LI-192SA/B quantum photometer (LI-COR, Lincoln, Nebraska, USA) until light readings fell below 1% of the surface PAR. The vertical light extinction coefficient (K_d) was calculated from the slope of a linear regression of the natural logarithm of PAR vs. depth. The water samples for nutrients, primary production, and zooplankton were collected from the surface to a depth of 2 m with a 2 m long column sampler (diameter, 50 mm; RIGO, Tokyo, Japan). Water samples were immediately filtered through Whatman GF/F glass fiber filters (Whatman, Clifton, New Jersey, USA) and was frozen at -30°C for nutrient analyses. The concentrations of $\text{PO}_4\text{-P}$ and $\text{NO}_3\text{-N}$ were analyzed using a continuous flow analyzer (AACS-II, BRAN + LUEBBE, Norderstedt, Germany).

Primary production was measured via short-term incubations using $\text{NaH}^{13}\text{CO}_3$ in the laboratory. Water samples were collected with an acrylic column sampler from the surface to a depth of 2.0 m and transported to the lab, where subsamples were transferred to six 50- or 100-mL bottles. A solution of $\text{NaH}^{13}\text{CO}_3$ (0.5 mg/L) was added to each bottle. The bottles were incubated for 1 h at six different light levels (0, 20, 50, 100, 300, or 1000 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in a water tank maintained at the in situ water temperature. After incubation, the particulate matter in each bottle was collected on precombusted GF/F filters under dim light. The concentrations of organic carbon and the $^{13}\text{C}:^{12}\text{C}$ isotope ratios of the samples were determined using a mass spectrometer with an in-line combustion furnace (Finnigan MAT DeltaPlus and Thermo Fisher Scientific Delta V

Advantage, Thermo Fisher, Waltham, Massachusetts, USA). The ^{13}C uptake by the phytoplankton in each bottle was used to generate a photosynthesis-irradiance ($P-I$) curve. Photosynthetic parameters obtained from the $P-I$ curves, such as the maximum rate of photosynthesis (P_{max}), were used to estimate primary production. Daily production per unit area per day was calculated using photosynthetic parameters, particulate organic carbon (POC, as the abundance of phytoplankton), water depth, surface light (PAR at depth 0), K_d , and the hourly incident solar radiation. Water samples for POC analysis were filtered onto precombusted glass-fiber filters (Whatman GF/F). POC was measured with a CHN analyzer (MT-5, Yanaco, Kyoto, Japan). The hourly incident solar radiation was obtained from the Kasumigaura Water Research Station of NIES ($36^\circ00.350'$ N, $140^\circ22.363'$ E). For more details on the methodology of measuring primary production with ^{13}C , see Takamura and Nakagawa (2016). Similar primary production measurements using POC have been adopted in some previous studies (e.g., Hama and Yanagi 2001, Yoshimizu et al. 2001).

Phytoplankton subsamples were fixed immediately with acid Lugol's iodine solution in the field. The cells or units of each phytoplankton taxon were counted under an inverted microscope with a Utermöhl chamber. Approximately 30 cells or units of each taxon were measured and biovolume was calculated based on the equation for the most similar geometric shape (Takamura and Nakagawa 2012). Phytoplankton were grouped into four major taxonomic groups: cyanobacteria, Bacillariophyceae, Chlorophyceae, and Cryptophyceae (Appendix S1: Fig. S3). To represent changes in the phytoplankton community composition, we conducted a

principal component analysis (PCA) on the biovolume of the four phytoplankton groups. We used only the first component (PC1), which accounted for 64.3% of the total variance. PC1 had a strong negative loading of cyanobacteria (-0.96) and weak negative loadings of Bacillariophyceae (-0.09), Chlorophyceae (-0.18), and Cryptophyceae (-0.17). PCA was conducted using the `prcomp` function in R.

Zooplankton samples were filtered through a 40- μm mesh plankton net (Takamura et al. 2017) and preserved with sugar-containing formalin at a final concentration of 4%. Zooplankton were counted in the laboratory using an inverted microscope and were identified to the species or genus level. We classified five functional groups: large cladocerans (>1.0 mm, e.g., *Diaphanosoma brachyurum*, *Daphnia galeata*), small cladocerans (<1.0 mm, e.g., *Bosmina* spp., *Moina micrura*), rotifers, calanoids, and cyclopoids. We used the abundance of those groups for the analysis (Appendix S1: Fig. S2). Adults were used in the analysis of calanoids and cyclopoids.

Convergent cross-mapping analysis

We used CCM to determine the causal relationships between primary production and environmental variables and zooplankton. Details of the CCM algorithm can be found in Sugihara et al. (2012). Briefly, CCM is based on Takens' theorem, which states that the essential information of a multidimensional dynamical system is retained in the time series of any single variable of that system. The theorem supports the use of a simplex projection (Sugihara et al. 2012), which predicts the dynamics of a process that is part of a larger system by using information from multiple lagged observations of that single process. In CCM, simplex projection is used to measure the extent to which the historical record of the response variable Y reliably estimates states of a potential forcing variable X (Tsonis et al. 2015). Variable Y is assumed to be causally forced by variable X if information from Y can be used to accurately forecast the dynamics of X . For example, if historical nutrient dynamics can be forecast using historical information about primary production, this would be indicative of causal forcing of primary production dynamics by nutrients. The predictive skill of cross mapping (cross-map skill) is quantified by calculating the correlation coefficient ρ between predicted and observed values of X . This procedure is repeated using a subset of the time series of X with different lengths L . The cross-map skill is expected to improve with the length of the time series L until it converges to a maximum level if two variables are causally coupled (i.e., convergence).

Before applying CCM, we determined the optimal embedding dimension (E) using a simple-projection (Sugihara et al. 2012, Tsonis et al. 2015). The best E for each time series was chosen from two to eight dimensions based on prediction skill (i.e., the dimension with the highest ρ). Using the best E , we next tested for the nonlinearity of the time series using an S-map (sequential locally weighted global linear map), which computes a local linear map between lagged coordinate vectors and a target variable (Sugihara et al. 2012). An S-map contains a nonlinear tuning parameter θ that affects the weights associated with individual coordinate vectors when fitting the local linear map. When $\theta = 0$, all weights are equal,

and the S-map is identical to an autoregressive model; values of θ greater than zero give greater weight to nearby vectors and thereby accommodate nonlinear behavior. We confirmed that all the variables displayed nonlinear dynamics.

For each link, we performed CCM using the best E and a fixed interval $\tau = 1$ month, and we calculated ρ using random subsamples of different L . However, most of our data showed seasonality, and synchronization driven by seasonality can misidentify causality (Cobey and Baskerville 2016). To distinguish causal effects from seasonality, we therefore performed a null test involving surrogate time series (Tsonis et al. 2015, Deyle et al. 2016a). Following the method used by Deyle et al. (2016a), we created surrogate time series having the same seasonal cycle as the actual driver, but with randomized anomalies. For a forcing variable $Z(t)$, we calculated the seasonal anomaly as the difference between the observed value $Z(t)$ and the monthly average Z (the average of all Januaries, Februaries, and so on). We then randomly shuffled the time indices of the seasonal anomalies. Adding the shuffled anomalies back to the season average gave a surrogate time series Z^* that had the same seasonal average as Z , but with random anomalies (Deyle et al. 2016a). We repeated this procedure 1,000 times to produce an ensemble of surrogates. Finally, we compared the ρ calculated from the real time series with the ρ values expected from the random surrogate time series. The causal relationship was considered to be significant only if the ρ at the maximum L ($\rho_{L_{\max}}$) calculated from the real time series was significantly greater than the 95th percentile of the ρ values computed from the surrogate time series. In this present study, we used a significance threshold of $P < 0.05$, but we considered a marginal significance ($0.05 \leq P < 0.1$) to be a weak causal relationship. All CCM analyses were conducted with Mathematica (version 10.2, Wolfram Research, Inc., Champaign, Illinois, USA).

Analyzing the relationships between zooplankton and pond smelt

To explore the relationships between zooplankton and planktivores, we focused on pond smelt, which is the most abundant planktivore in Lake Kasumigaura. Pond smelt is the most commercially important species in the lake and accounts for more than 30% of the total commercial catch.

We calculated catch-per-unit-effort (CPUE), as a measure of the relative abundance of pond smelt using the Annual Statistics of Fishery and Aquaculture Production of the Ministry of Agriculture, Forestry and Fisheries. The CPUE (kg/d) was calculated by dividing the annual trawl catch (kg/yr) by total number of days fished that licensed fishermen worked on lakes throughout a year (d/yr). We calculated the annual CPUE of pond smelt only between 1996 and 2006, because fishing effort data have not been available since 2007 (Appendix S1: Fig. S4).

Because the annual CPUE of pond smelt was a short time series ($N = 11$), we did not apply CCM to analyze the relationships between zooplankton and pond smelt. Instead, we used a correlation analysis. In correlation-based analysis, bottom-up control should result in a positive correlation between fish and zooplankton, whereas top-down control should result in a negative correlation between fish and zooplankton (Richardson and Schoeman 2004). Although we

recognize that simple correlation does not imply causation, we wanted to examine specifically how the results of CCM linked to the abundance of planktivores in the system.

Using a generalized least-squares regression (GLS) model, we separately examined the relationships between the annual mean abundance of each zooplankton functional group and the annual CPUE of pond smelt. To consider temporal autocorrelation, we included a term that corrected for first-order autoregressive processes, AR(1), in the GLS models. Maximum likelihood was used for estimating the model parameters. GLS models were analyzed using the `gls` function from the `nlme` package in R. All regression analyses were conducted with R (version 3.2.3; R Core Team, 2015).

RESULTS

CCM identified some drivers as being significantly causal. $\text{NO}_3\text{-N}$ and phytoplankton PC1 were identified as significant forcing variables (Figs. 2, 3, Table 1) because the measured $\rho_{L_{\max}}$ between these variables and primary production significantly exceeded the null expectation value (Appendix S1: Fig. S5). The fact that the causal influence of primary production on the light-extinction coefficient was statistically marginal ($P = 0.062$) suggested that the light-extinction coefficient was weakly forced by primary production. CCM did not detect significant causal effects of water temperature and $\text{PO}_4\text{-P}$ on primary production, although the linear relationship between water temperature and primary production was significant (Table 1).

CCM did not detect a significant causal effect of zooplankton on primary production (Figs. 2, 3, Table 1, Appendix S1: Fig. S6). Instead, rotifers and cyclopoids were causally forced by primary production. Furthermore, cyclopoids were causally influenced by rotifers, although the linear correlation was not significant. However, the fact that the causal influence of rotifers on primary production was statistically marginal ($P = 0.078$) suggested that primary production was weakly forced by rotifers. For large-cladocerans, small-cladocerans, and calanoids, CCM did not detect causal links in either direction, although the linear relationship between primary production and either large cladocerans or small cladocerans was significant.

The causal networks between phytoplankton abundance (we used POC) and other variables differed somewhat from those between primary production and other variables, but CCM did not detect top-down forces (Appendix S1: Table S1, Figs. S7–S9). Phytoplankton abundance was forced by $\text{NO}_3\text{-N}$ and the light-extinction coefficient. There was also a bidirectional interaction between phytoplankton abundance and phytoplankton PC1. Whereas cyclopoids were forced by phytoplankton abundance, CCM did not detect significant causal relationships between phytoplankton abundance and other zooplankton groups in either direction.

The GLS models revealed significant positive relationships between the abundances of rotifers and cyclopoids vs. pond smelt CPUE (Fig. 4, $r^2 = 0.54$ and 0.36 , respectively). Other zooplankton groups were not related to pond smelt CPUE.

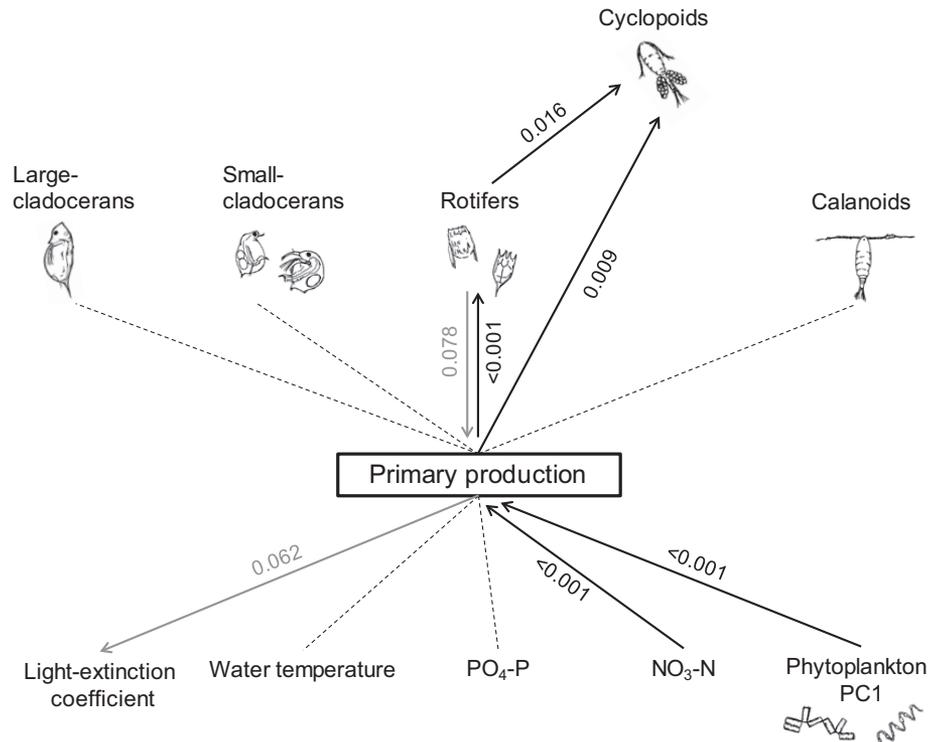


FIG. 2. Schematic summarizing the significant causal relationships between primary production and other variables inferred from the convergent cross-mapping (CCM) analyses. The direction arrows indicate the causality direction. Black and gray arrows indicate significant ($P < 0.05$) and marginally significant ($0.05 \leq P < 0.01$) causal relationships, respectively. The numbers near the arrows indicate the P values (see also Table 1). The dashed lines represent no significant causal association between the variables.

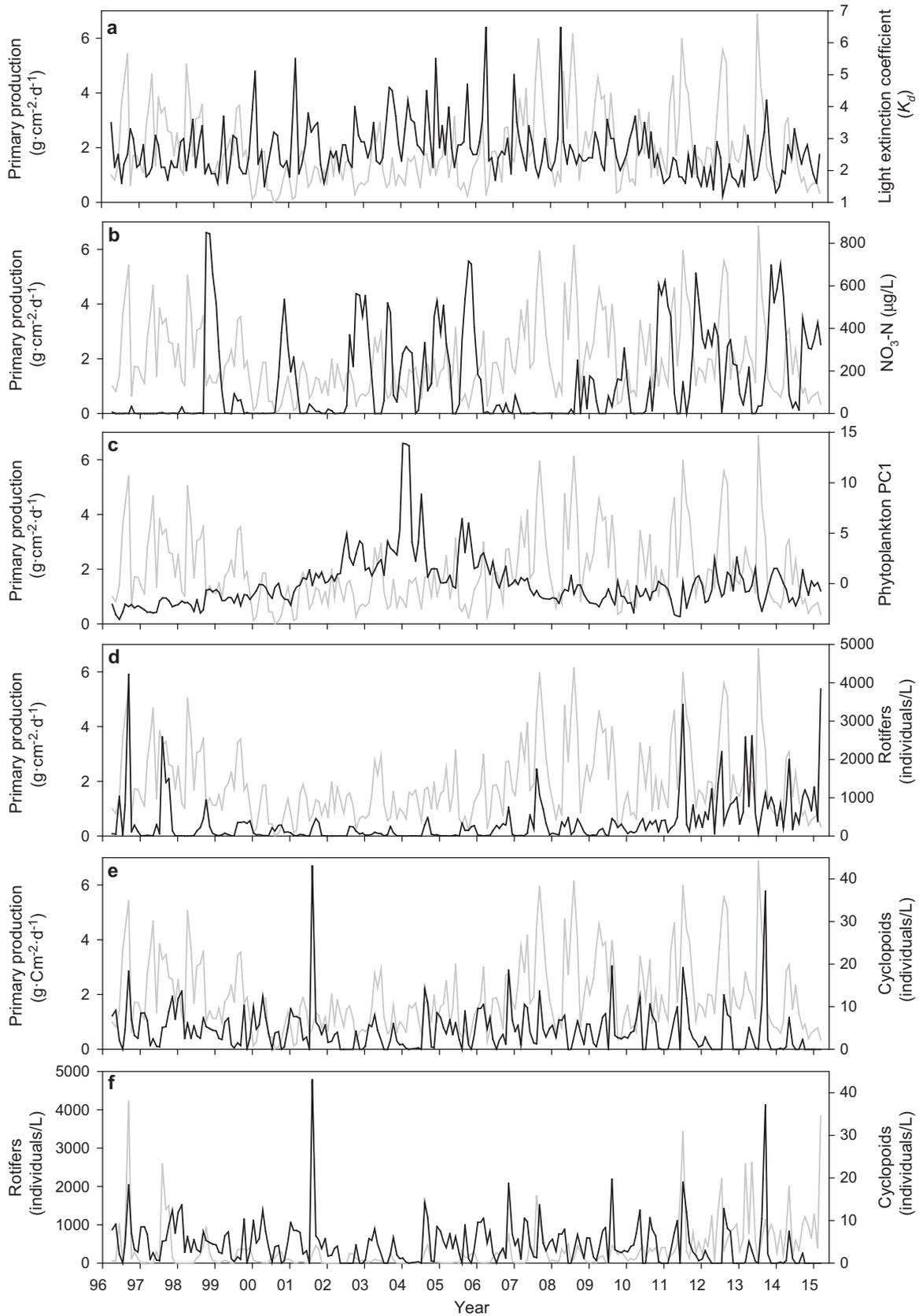


FIG. 3. Long-term monthly variations (from April 1996 to March 2015) of the two variables for which CCM detected significant casual relationships: (a) primary production vs. light extinction coefficient, (b) primary production vs. $\text{NO}_3\text{-N}$, (c) primary production vs. phytoplankton PC1, (d) primary production vs. rotifers, (e) primary production vs. cycloids, and (f) rotifers vs. cycloids. Note different axes (the left axis is shown in gray and the right axis is shown in black).

TABLE 1. Summary of results of the convergent cross-mapping (CCM) and simple linear correlation analyses for the relationships between primary production and other variables.

<i>X</i>	<i>Y</i>	Cross-map skill (<i>X</i> → <i>Y</i>)			Cross-map skill (<i>Y</i> → <i>X</i>)			Linear cross-correlation (<i>X</i> and <i>Y</i>)
		<i>E</i>	ρ_{Lmax}	<i>P</i>	<i>E</i>	ρ_{Lmax}	<i>P</i>	<i>r</i>
Light-extinction coefficient	primary production	7	0.14	0.223	3	0.33	0.062	−0.27
Water temperature	primary production	6	0.34	0.999	3	0.35	0.153	0.37
PO ₄ -P	primary production	6	0.15	0.999	3	0.36	0.714	−0.05
NO ₃ -N	primary production	7	0.27	0.000	3	0.35	0.982	−0.37
Phytoplankton PC1	primary production	3	0.26	0.000	3	0.36	0.563	−0.32
Large-cladocerans	primary production	7	0.23	0.476	3	0.34	0.864	0.15
Small-cladocerans	primary production	8	0.23	0.215	3	0.36	0.285	0.21
Rotifers	primary production	4	0.23	0.078	3	0.31	0.000	0.27
Calanoids	primary production	8	0.10	0.954	3	0.25	0.980	0.00
Cyclopoids	primary production	3	0.20	0.315	3	0.19	0.009	0.22
Cyclopoids	rotifers	3	0.22	0.352	4	0.24	0.016	0.10

Notes: *E* is the best embedding dimension and ρ_{Lmax} is the cross-map skill (ρ , Pearson correlation between observed and predicted values) obtained at the maximal library length (*L*). The statistical significance of CCM was determined using a randomization test involving surrogate time series; *r* is the linear cross-correlation. Boldface ρ_{Lmax} values indicate significance at $P < 0.05$.

DISCUSSION

Overall, our causality analysis, which took into consideration seasonality effects, detected only significant causal forcing associated with bottom-up control of primary production in Lake Kasumigaura (Table 1, Fig. 2). We found no measurable evidence of top-down control of primary production by zooplankton, but instead we detected causal influences of primary production on rotifers and cyclopoids, and we detected a causal influence of rotifers on cyclopoids. To the best of our knowledge, this is the only study that has demonstrated causal linkages between nutrient, primary production, and zooplankton via bottom-up processes. Furthermore, our correlation analysis showed that rotifers and cyclopoids were positively correlated with pond smelt CPUE (Fig. 4). This result suggests that bottom-up linkages from nutrients to zooplankton can be a key mechanism supporting high planktivorous fish abundance in shallow eutrophic lakes.

The findings in this study need to be carefully interpreted. First, the links that were not significant in our CCM analysis should not be interpreted as significant evidence of no causal forcing. The results instead indicate one of three things: (1) there was no causal forcing, (2) synchrony due to a shared cyclical forcing variable was too strong to detect the causal link (although we considered the effect of seasonality), or (3) causal forcing was too weak to detect given the existing time series. With respect to reason 3, large observation errors could affect the detection of causal signals. Furthermore, our CCM did not quantify the interaction sign and strength of the causal relationships. Because our analysis revealed only the presence and direction of the causal relationships, it may be inappropriate to simply compare our results with previous studies on primary production. Some previous studies on lake ecosystems (e.g., Ives et al. 2003, Hampton et al. 2008) quantified the interaction strengths among variables from long-term data sets using MAR or MARSS models. For example, Walsh et al. (2016) showed that water quality was determined by water temperature, phosphorus concentration, and *Daphnia pulicaria* abundance, but the relative strengths of these effects were

−0.33, −0.21, and, 0.10, respectively. Although these methods can identify fixed interactions in the presence of noise and can be useful when systems change slowly, it has been noted that they are not suitable for predicting rapid changes because these methods do not explicitly address state dependence (i.e., non-linearity; Deyle et al. 2016b, McGowan et al. 2017). Rather, the advantage of this study is that, unlike regressive models, it determines the direction of the causal interactions when the variables are mutually coupled. Deyle et al. (2016b) recently developed a multivariate S-map method to quantify time-varying interactions; this method has been shown to be robust to observational errors. As mentioned in Deyle et al. (2016b), combinations of autoregressive models, CCM, the multivariate S-map (see also Suzuki et al. 2017), and other approaches would lead to more detailed understanding of the underlying mechanisms.

Previous studies based on correlation have demonstrated that primary production in Lake Kasumigaura during 1981–1989 was controlled by water temperature and solar radiation (Takamura et al. 1987, Takamura and Aizaki 1991), but photosynthesis in the growing season was limited by nitrogen (Takamura et al. 1992). Primary production during 1982–2006 was limited by total nitrogen concentrations and reductions in light availability caused mainly by increases in suspended solids, probably due to sediment dredging (Takamura 2012). In contrast, other studies have been unable to find any relationship between zooplankton and primary production, although the temporary occurrence of *D. galeata* in the late 1980s reduced phytoplankton biomass (not primary production) in Lake Kasumigaura (Hanazato and Aizaki 1991). Our causality analysis identified not only the causal drivers of primary production but also the interactive links between primary production and the zooplankton community, relationships that correlation analysis had not previously detected. We thus highlighted the effectiveness of CCM in elucidating complex trophic relationships in eutrophic lakes as well as the importance of long-term monitoring data.

We showed that primary production was causally controlled by NO₃-N and not by other environmental factors (Fig. 2). Although most temperate, freshwater lakes are

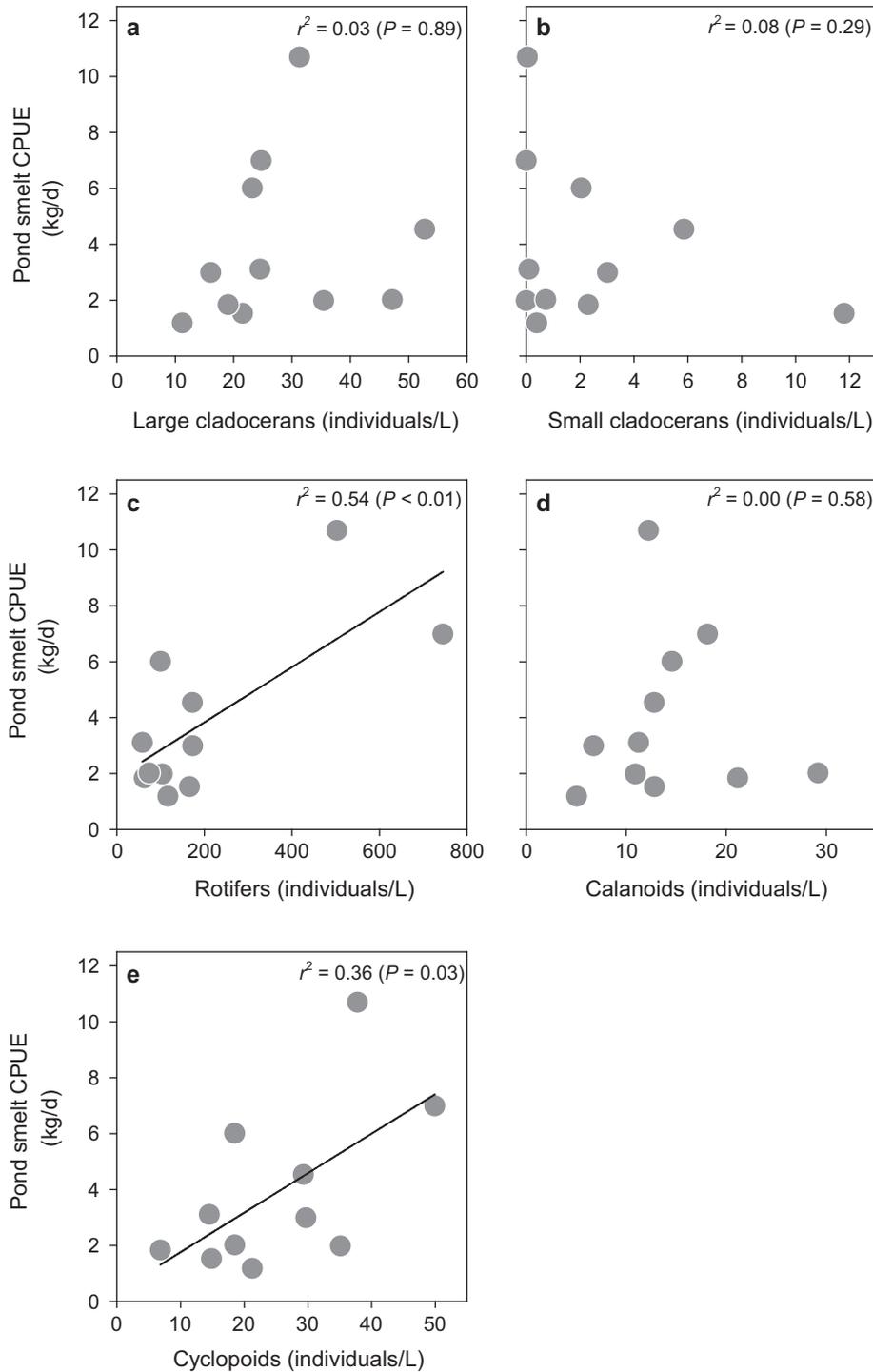


FIG. 4. Linear correlations between the annual mean abundances of (a) large cladocerans, (b) small cladocerans, (c) rotifers, (d) calanoids, and (e) cyclopoids, and the annual catch per unit effort (CPUE) of pond smelt over the 11-yr study (1996–2006). The solid lines represent significant relationships ($P < 0.05$) detected by generalized least-squares regression (GLS).

considered to be phosphorus-limited (Schindler 1977), limitation of primary production by nitrogen and co-limitation by nitrogen and phosphorus have been reported (Elser et al. 2009, Pace and Lovett 2013). Nitrogen limitation has been reported to occur at ratios by mass of total nitrogen (TN) to total phosphorus (TP) <10 (Sakamoto 1966), <13 (Smith 1979), and <14 (Downing and McCauley 1992). In Lake

Kasumigaura, the annual mean TN:TP of 9.7 ± 2.1 (mean \pm SD) between 1996 and 2015 suggests that production in the lake is nitrogen limited. Our CCM results suggest the possibility that nitrogen can limit primary production, even in temperate eutrophic lakes.

One possible explanation for nitrogen limitation could be that Lake Kasumigaura is a hyper-eutrophic, phosphorus-rich

lake. The internal phosphorus loading of this lake has been reported to exceed external loading (Havens et al. 2001), although few studies have quantified the internal nitrogen loads. Finlay et al. (2013) reported that increased phosphorus inputs can stimulate denitrification and thereby increase rates of nitrogen removal. External and internal phosphorus loading might promote nitrogen limitation. An alternative explanation is that the production of dissolved phosphorus via degradation of organic matter in the waters of Lake Kasumigaura could relieve phosphorus limitation of phytoplankton (Shinohara et al. 2016). However, because $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ seem to vary annually as well as seasonally (Appendix S1: Fig. S1), informed nutrient management will require consideration of other factors that affect nutrient dynamics, including water level regulation, sediment dredging, and floods.

Because phytoplankton have species-specific traits, such as light use efficiency (Zwart et al. 2015, Lehtinen et al. 2017), phytoplankton composition can affect primary production (Darchambeau et al. 2014). Our CCM results suggest that primary production was forced by phytoplankton composition (Table 1, Fig. 2). Takamura and Aizaki (1991) reported that, at the end of the 1980s, primary production in Lake Kasumigaura decreased because of a shift in phytoplankton species composition, in spite of the increase of TN concentrations. Phytoplankton PC1 was composed mainly of cyanobacteria that were dominated by non-nitrogen-fixing species (mainly *Pseudanabaena*, *Planktothrix*, and *Microcystis*) (Takamura and Nakagawa 2012). The appearance and disappearance of cyanobacteria can thus be one of the key drivers determining primary production in a hyper-eutrophic lake. Moreover, our CCM results suggest that light availability was weakly forced by primary production, whereas phytoplankton abundance was forced by light availability (Appendix S1: Table S1, Fig. S7). These findings are consistent with previous findings showing that increases in phytoplankton abundance due to nutrient loading can restrict light availability (through shading) and determine the proportion of cyanobacteria in the phytoplankton community in shallow eutrophic lakes (Kosten et al. 2012).

We did not detect top-down control of primary production by zooplankton. Rather, our results suggest bottom-up control of rotifers and cyclopoids by primary production (Fig. 2). This result is partly consistent with some comparative and whole-lake experimental studies showing that an increase of primary production increases the abundance or biomass of rotifers, cyclopoids, and cladocerans (Pace 1986, Pace et al. 1998, Carpenter et al. 2001, Yoshida et al. 2003). There are three possible explanations for the dominance of bottom-up forcing in Lake Kasumigaura. First, primary production can respond more strongly to nutrient enrichment in lakes with three trophic levels (planktivores, herbivores, and phytoplankton) than in lakes with a fourth trophic level of piscivores (Carpenter et al. 2001). Considering that there are few piscivorous fish species and that omnivorous and planktivorous fish species are dominant in many Japanese lakes, including Lake Kasumigaura (Matsuzaki et al. 2016), the regulation of primary production by grazing may be weak in Japanese lakes. Second, lake characteristics (shallow and temperate) could promote the dominance of bottom-up forces, because production in relatively

warm and species-rich waters is controlled primarily by bottom-up processes (Frank et al. 2007). Shallow depths, which promote efficient nutrient recycling and physical variability, are considered to contribute to efficient energy transfer from primary production to secondary production (Costanza et al. 1993). Third, food quality, particularly the proportions of edible and inedible algae within the phytoplankton, might affect zooplankton grazing or competition among zooplankton species (Brett and Goldman 1997, Yoshida et al. 2003). In eutrophic lakes, the dominance of cyanobacteria strongly inhibits cladocerans, whereas rotifers have the ability to grow and reproduce on a diet of cyanobacteria (Fulton and Paerl 1987, Davis et al. 2012). Differences in food utilization due to differences between feeding types might explain why only rotifers and cyclopoids are forced by primary production.

Interestingly, our CCM suggests that primary production was weakly forced by rotifers (i.e., bidirectional interactions). Small-bodied zooplankton have higher mass-specific rates of nutrient recycling than large zooplankton, and their excretion can alter the balance of nitrogen and phosphorus supplied to phytoplankton (Hambright et al. 2007). Moreover, rotifers exhibit high species richness and functional diversity with a broad range of feeding types and sizes (Arndt 1993). Considering that there was no measurable evidence of a causal influence of rotifers on phytoplankton abundance (Appendix S1: Fig. S7), rotifers may stimulate phytoplankton carbon fixation by their nutrient cycling and functional diversity. In other words, our findings might suggest the existence of feedback loops between rotifers and primary production (Carpenter et al. 1992). Future research should target better understanding of the role of rotifers, which transfer carbon in the food web of hyper-eutrophic lakes.

The applicability of POC as a measure of phytoplankton abundance should be discussed. POC can include not only phytoplankton but also non-phytoplankton particles. Chlorophyll *a* is a more conventional and common measurement of phytoplankton abundance. However, phytoplankton use a variety of photosynthetic pigments in addition to chlorophyll *a*, to capture light. These accessory pigments potentially influence carbon conversion (Riemann et al. 1989). Lake Kasumigaura is hyper-eutrophic, and POC can therefore include non-phytoplankton particles. Because there was a positive relationship between POC and chlorophyll *a* (Pearson $r = 0.74$), both variables are metrics of phytoplankton abundance. The advantage of our study was the direct measurement of the amount of carbon fixed per unit time and per unit water volume, even if POC included non-phytoplankton particles. We believe that the rate of carbon fixation influenced rotifers and cyclopoids in this hyper-eutrophic lake.

Many studies have reported that primary production supports fish production, but few have explored the primary-production–zooplankton–fish-production linkages (e.g., Downing et al. 1990, Karlsson et al. 2009). In this study, the zooplankton groups that were causally influenced by primary production were the same groups that were correlated with pond smelt CPUE (Figs. 2, 4). The relationship between rotifer abundance and pond smelt CPUE appears to be driven by two points (Fig. 4c). Although we did not analyze this relationship between 1996 and 2006, the annual

mean abundance of rotifers after 2007 was similar to or somewhat higher than the abundance of these two points. This interpretation can also be supported by the work of Tokoro (2016), who reported that the catch of pond smelt has increased since 2007. Another critical question that emerged from our correlation analysis is whether pond smelt increase rotifers and cyclopoids or vice versa. It is well known that planktivorous fish feed selectively on large cladocerans, and the effect of that feeding in turn increases the abundance of relatively small herbivorous species, in particular, rotifers (e.g., Gilbert 1988). However, we did not detect such causal relationships. Our results thus suggest the existence of bottom-up linkages, not only between nutrients, primary production, and zooplankton, but also between nutrients, primary production, zooplankton, and fish, as reported by Ware and Thomson (2005) and Bunnell et al. (2014).

With respect to bottom-up linkages, microzooplankton, such as rotifers, are important food sources for the larval and juvenile stages of pond smelt, which experience relatively high mortality (Yoshioka et al. 1994). The abundance of these zooplankton is considered to be the most important factor determining the abundance of pond smelt in Lake Kasumigaura (Kumamaru 2003, Tokoro 2016). Interestingly, the fact that cyclopoids were causally influenced by both primary production (directly) and rotifers (indirectly) suggests that multiple pathways might help stabilize pond smelt populations via compensatory processes (Connell and Ghedini 2015). Our study provides new insights about energy transfer from primary production to planktivores. Specifically, rotifers and cyclopoids, but not cladocerans, may support planktivore biomass in hypereutrophic lakes.

Further research is needed to assess the robustness of the conclusions of the present study. First, we did not analyze the causal relationships between zooplankton and pond smelt CPUE, and our analysis was based on pond smelt data obtained from only 1996–2006. A monthly monitoring scheme would be required to evaluate the pond smelt stocks because of the lack of a long-term monthly data set on this species. However, application of CCM would have been possible if there had been a short time series data set with spatially replicated data (Clark et al. 2015). Second, we did not address zooplankton biomass. Because zooplankton abundance and biomass sometimes respond differently to nutrient enrichment and fish abundance (Pace 1986, Yoshida et al. 2003), zooplankton biomass is worth estimating in future studies. Finally, we may have oversimplified the processes and interactions within the lake ecosystem. Bacteria and protozoa can play an important role in energy transfer to zooplankton through the microbial food web (Havens 2014). These processes should be taken into consideration in the causality analysis to fully understand the mechanisms determining primary production and the relationships between primary production and higher trophic levels.

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